UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA RÉPARTITION SPATIALE DES COUPES FORESTIÈRES ET SES EFFETS SUR LA DISTRIBUTION ET LE COMPORTEMENT ALIMENTAIRE DES OISEAUX EXCAVATEURS EN FORÊT BORÉALE

MÉMOIRE

PRÉSENTÉ

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DE LA MAÎTRISE EN BIOLOGIE

PAR

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AVANT-PROPOS

Ce mémoire comporte deux chapitres rédigés sous forme d'articles. À titre de candidate à la maîtrise, j'ai procédé à la supervision et à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de première auteure. Ces deux articles seront soumis à des revues scientifiques arbitrées : 1) Effects of spatial configuration of clear-cuts on the abundance and occurrence of primary cavity excavator birds in the boreal forest of northwestern Quebec et 2) Anthropogenic edges: their influence on the American Three-toed Woodpecker (*Picoides dorsalis*) foraging behaviour in managed boreal forests of Quebec. Mon directeur de recherche, Pierre Drapeau, ainsi que mon codirecteur, Louis Imbeau, en sont les coauteurs.

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Article 1

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LISTE DES ACRONYMES

-2ll	-2 log-likelihood
AAC	Annual allowable cut
AIC_c	Akaike's second-order information criterion
All Wo.	All woodpeckers
Atwo	American Three-toed Woodpecker
Bbwo	Black-backed Woodpecker
Bfi	Balsam fir
Boch	Boreal Chickadee
Bsp	Black spruce
CPRS	Coupe avec protection de la régénération et des sols
Cut_75	Area of clear-cuts in the 75 m radius
Cut_1000	Area of clear-cuts in the 1000 m radius
Cut_2000	Area of clear-cuts in the 2000 m radius
DBH	Diameter at breast height
Deci	Basal area of deciduous trees
Dist	Distance to undisturbed mature forest > 500 ha
Edge_75	Length of edges in the 75 m radius
Edge_1000	Length of edges in the 1000 m radius
Edge_2000	Length of edges in the 2000 m radius
Fo_75	Area of mature forests in the 75 m radius
Fo_1000	Area of mature forests in the 1000 m radius
Fo_2000	Area of mature forests in the 2000 m radius
Hawo	Hairy Woodpecker
K	Number of parameter in regression models
Large Wo.	Large woodpeckers
Logs	Basal area of downed woody debris
Lt_20	Basal area of large live trees (DBH $\geq$ 20 cm)
Nofl	Northern Flicker
Rbnu	Red-breasted Nuthatch

SE	Standard error
Small Wo.	Small woodpeckers
Snags	Basal area of snags
Tas	Trembling aspen
Wbi	White birch
WCE	Weak cavity excavators
Ybsa	Yellow-bellied Sapsucker

RÉSUMÉ

Les coupes agglomérées et en mosaïque constituent deux stratégies d'aménagement qui diffèrent grandement de par la quantité ainsi que la configuration des habitats résiduels à l'échelle du paysage. Par ailleurs, des différences dans la configuration de la forêt résiduelle engendrent, entre autres, la création de bordures d'origine anthropique, celles-ci pouvant affecter la qualité des peuplements forestiers ainsi que le comportement des espèces animales associées aux forêts mûres et surannées. Le premier chapitre de ce mémoire a pour objectif de documenter de quelle manière le groupe fonctionnel des excavateurs primaires de cavités répond (1) à la quantité de forêts résiduelles à l'échelle du paysage, (2) à la configuration des peuplements forestiers résiduels à l'échelle du paysage et (3) à la rétention d'attributs de structure caractérisant les forêts surannées (arbres vivants de grand diamètre, chicots et débris ligneux) dans les peuplements résiduels des patrons de coupes agglomérées et en mosaïque. Le deuxième chapitre de ce mémoire vise quant à lui (1) à déterminer quelles sont les caractéristiques des arbres utilisés pour l'alimentation du Pic à dos rayé (*Picoides dorsalis*), (2) à déterminer si les pics s'alimentent en fonction de la disponibilité des bons substrats d'alimentation dans les bordures de coupes et (3) à caractériser le patron de déplacement des pics lors de leur quête alimentaire à proximité des lisières. L'aire d'étude se situe dans la zone de la pessière noire à mousses, dans la région du Nord-du-Québec (49° 12' à 50° 09' de latitude nord et 75° 09' à 76° 37' de longitude ouest). Dans le cadre du premier chapitre, nous avons échantillonné neuf espèces d'oiseaux excavateurs de cavités dans 160 stations réparties également entre les peuplements résiduels des coupes agglomérées et en mosaïque. L'échantillonnage a été réalisé avec les méthodes des points d'écoute et des points d'appel dans le but de détecter le plus grand nombre d'individus possible. Les attributs de structure ainsi que les variables du paysage ont également été caractérisés pour chacune des stations. En ce qui concerne le deuxième chapitre, nous avons réalisé des suivis focaux de pics à dos rayé à l'intérieur de 18 bordures de coupes. Un inventaire des arbres morts sur pied et au sol a également été réalisé dans les lisières où des suivis focaux ont été préalablement réalisés. Nos résultats montrent que le Pic à dos rayé et la Mésange à tête brune (*Poecile hudsonicus*) avaient une occurrence plus forte dans les habitats résiduels des coupes en mosaïque alors que le Pic Flamboyant (*Colaptes auratus*) était plus abondant dans les habitats linéaires des coupes agglomérées. De plus, autant les variables locales que celles du paysage étaient importantes pour les espèces à l'étude. D'autre part, bien que les bons substrats d'alimentation pour le Pic à dos rayé étaient plus abondants à proximité des lisières, les pics évitaient tout de même de s'alimenter à cet endroit. Finalement, bien que les habitats linéaires des coupes agglomérées sont susceptibles de représenter des habitats sub-optimaux, ils sont néanmoins utilisés par la majorité des espèces à l'étude. Ainsi, la rétention, de façon permanente, de ces habitats linéaires ainsi que de massifs forestiers de plus grande superficie pourrait améliorer les conditions forestières et ainsi faire en sorte de maintenir ce groupe important d'espèces en zones aménagées.

Mots clés : *excavateurs primaires de cavités, pics, coupes en mosaïque, coupes agglomérées*

INTRODUCTION GÉNÉRALE

1.1 Fragmentation et perte d'habitat : les problèmes liés à l'exploitation forestière

En Amérique du Nord, les écosystèmes forestiers boréaux sont modelés par différents régimes de perturbations naturelles qui ont cours à plus ou moins grande échelle (Johnson et al. 2003; Bergeron et al. 2004). Le feu est sans contredit le principal agent façonnant les forêts boréales conifériennes et ce dernier affecte le territoire différemment selon sa fréquence, sa sévérité ainsi que la superficie brûlée (Bergeron et al. 2001; 2002). Un changement dans ces trois composantes peut engendrer une modification de la distribution des classes d'âge, de la composition ainsi que de la structure forestière (Bergeron et al. 2001). Les paysages forestiers sont donc loin d'être homogènes; au contraire, il s'agit d'une matrice composée d'un assemblage d'habitats différents en structure et en âge (Harper et al. 2002). Historiquement, les espèces animales inféodées à la forêt boréale ont évolué dans un système où les massifs forestiers sont naturellement fragmentés (Schmiegelow et al. 1997; Drapeau et al. 2000; Imbeau et al. 2001). Selon Andrén (1994), la fragmentation peut se définir comme un processus de subdivision d'un habitat continu en plus petits morceaux survenant dans les écosystèmes par l'entremise de perturbations naturelles ou anthropiques. En plus d'engendrer une réduction de la mobilité des oiseaux ainsi qu'une baisse du succès reproducteur (Robinson et al. 1995), la fragmentation est également susceptible d'affecter le comportement social de plusieurs espèces en réduisant le partage d'information entre individus (Ahlering et Faaborg 2006). Le partage d'information est un facteur qui, conjointement avec la qualité de l'habitat, semble jouer un rôle majeur dans le processus de sélection de sites de reproduction chez certaines espèces (Ward et Schlossberg 2004). Par ailleurs, la fragmentation engendre la diminution de la taille des peuplements forestiers résiduels ainsi que l'isolement accru de ceux-ci, ces deux phénomènes exerçant une pression supplémentaire sur les espèces vivant à l'intérieur des forêts morcelées (Haila 1999). D'après Andrén (1994), cette pression se fait ressentir plus fortement lorsque la quantité d'habitat originel est en deçà d'un seuil critique, fixé entre 10 et 30%. Mönkkönen et Reunanen (1999) nous invitent par contre à la prudence en affirmant que le seuil critique dépend de la nature de la matrice entourant les fragments d'habitat ainsi que de l'échelle à laquelle le phénomène est

étudié. En effet, la perception du paysage par un insecte nécessitant quelques hectares et un oiseau requérant plusieurs kilomètres carrés pour maintenir des populations viables est bien différente vu leurs échelles opérationnelles fort distinctes (Haila 1999; Mönkkönen et Reunanen 1999). De plus, chaque espèce réagit distinctement à la fragmentation, dépendamment de sa capacité à se mouvoir, de ses besoins en terme d'habitat (Mönkkönen et Reunanen 1999) et de sa capacité à utiliser un habitat alternatif. En d'autres termes, cela renvoie à la difficulté de généraliser les résultats à travers les paysages et les régions géographiques (Mönkkönen et Reunanen 1999).

Depuis plusieurs années, l'industrie forestière est devenue un acteur important en zone de pessière noire à mousses (Nappi 2000; Drapeau et al. 2002), celle-ci engendrant une perte et une fragmentation artificielle des forêts matures. La perte nette d'habitat, malgré qu'elle soit souvent décrite comme étant temporaire, affecte néanmoins plusieurs espèces animales, particulièrement celles qui sont associées aux vieilles forêts (Kouki et al. 2001). En zone boréale coniférienne, les peuplements comptant la plus grande diversité d'espèces de forêt mature sont ceux âgés entre 100 et 150 ans (Drapeau et al. 2003). Les rotations forestières plus courtes que le cycle naturel des feux conduisent à la diminution de la proportion de forêts mûres fermées ainsi qu'à la perte des forêts anciennes et surannées, ces facteurs menant par conséquent à la perte de nombreuses espèces associées aux vieilles forêts (Drapeau et al. 2003). En somme, l'application généralisée de la CPRS (coupe avec protection de la régénération et des sols), ou d'autres traitements produisant une forêt équienne, résulte à long terme en un rajeunissement et une uniformisation de la mosaïque forestière qui est naturellement constituée de peuplements d'âge, de structure et de composition variés (Harper et al. 2002).

D'autre part, l'aménagement forestier traditionnel est réalisé sans égards aux processus façonnant le paysage (Haila 1999). Par exemple, au Québec, il n'existe aucune politique de rétention d'arbres verts ou d'arbres morts sur pied (chicots) au sein des aires de récolte. Le Règlement sur les normes d'intervention dans les forêts publiques (RNI) du ministère des Ressources naturelles du Québec (MRN 2003) stipule en ce sens que le volume de matière ligneuse utilisable mais non récoltée ne peut excéder 3,5m³/hectare en moyenne

dans les CPRS pour éviter le gaspillage de matière ligneuse. Par contre, lors d'un incendie forestier, certains secteurs sont épargnés et les arbres qui s'y trouvent peuvent demeurer intacts ou être partiellement brûlés, le feu ne sévissant pas avec la même intensité sur tout le territoire (Leduc et al. 2000). Ces îlots agissent alors comme refuges pour les espèces à faible capacité de dispersion en plus d'augmenter l'hétérogénéité du peuplement en régénération (Haeussler et Kneeshaw 2003). En forêt boréale, le feu crée des conditions uniques d'habitat car c'est à cet endroit qu'est générée la plus grande quantité d'arbres morts (Nappi 2000; Drapeau et al. 2002). Les CPRS, qui entraînent la perte de ces attributs d'habitat, risquent donc d'affecter négativement le cortège d'espèces animales dépendantes de ces éléments de structure.

1.2 Lisières naturelles et d'origine anthropique : quelles sont les différences?

Les perturbations naturelles en milieu forestier engendrent des peuplements à différents stades successionnels. Ces habitats contrastés, tant par leur composition, leur structure et leur dynamique (Wiens 1989), sont juxtaposés et délimités par des lisières naturelles, ou écotones. En l'absence de perturbations naturelles, les facteurs abiotiques tels que la topographie et le type de sol vont générer des différences dans la composition forestière et ainsi créer des zones de transition naturelle entre les peuplements (Forman et Godron 1986). Par ailleurs, il existe, au sein des bordures attenantes à deux milieux contrastés tels qu'une forêt fermée et un milieu ouvert, un microclimat différent des conditions qui prévalent à l'intérieur de la forêt (McCollin 1998; Matlack et Litvaitis 1999; Brotons et al. 2001). Le taux d'humidité y est en effet plus faible et la radiation solaire plus élevée; cela se reflète sur la structure de la végétation et sur les espèces animales et végétales présentes dans ce type de milieu (Esseen et Renhorn 1998; Villard 1998; Matlack et Litvaitis 1999; Rheault et al. 2003).

L'aménagement forestier extensif en forêt boréale mène toutefois à la création de lisières qui ne ressemblent en rien à celles générées par la fragmentation naturelle des forêts. Elles sont en effet très abruptes et constituées d'un mur d'arbres matures qui sont de hauteur

semblable et disposés de façon uniforme, en plus d'être réparties assez arbitrairement sur le territoire, sans égards aux caractéristiques naturelles du paysage (Matlack et Litvaitis 1999). Ces bordures diffèrent aussi par leur longueur démesurée ainsi que par les caractéristiques de l'habitat adjacent nouvellement créé, une coupe récente étant un milieu plus hostile qu'un brûlis à l'intérieur duquel subsiste une grande quantité de chicots et plusieurs îlots d'arbres verts ou partiellement brûlés (Leduc et al. 2000; Haeussler et Kneeshaw 2003; Harper et al. 2004).

Les lisières d'origine anthropique semblent par ailleurs plus sensibles aux forts vents que les lisières naturelles, tel que montré par un très haut taux de chablis dans les bordures adjacentes à des coupes forestières récentes (Franklin et Forman 1987; Ruel et al. 2001; Mascarúa-López et al. 2006). Esseen (1993) a montré que le taux de mortalité des arbres pouvait atteindre 25% dans les peuplements résiduels de un hectare (ha) et jusqu'à 95% dans les peuplements de 1/16 ha suite à l'ouverture de la forêt par la coupe. Darveau et al. (1995) ont aussi montré qu'en forêt boréale, le taux de mortalité des arbres dans les habitats linéaires suivant une coupe était en moyenne de 23%. D'autre part, les travaux de Ruel et al. (2001) ont également montré que la quantité de chablis dans les habitats linéaires riverains était corrélée à la vitesse des vents soufflant perpendiculairement aux bandes riveraines.

1.3 Chicots et arbres vivants de gros diamètre : des attributs d'habitat essentiels

Les gros arbres vivants ainsi que les chicots constituent des micro-habitats importants pour plusieurs espèces de mammifères, d'oiseaux et d'amphibiens (Raphael et White 1984; Nappi 2000; Darveau et Desrochers 2001; Bevis et Martin 2002). Il existe également toute une myriade d'invertébrés qui colonisent les chicots tels que les insectes perceurs de xylème (longicornes) ainsi que les xylophages subcorticaux (scolytes) (Germain et al. 1996; Saint-Germain et al. 2004; Saint-Germain et al. 2006). Parmi la faune aviaire, les oiseaux excavateurs sont particulièrement sensibles à la récolte forestière puisqu'ils sont dépendants des arbres vivants de gros diamètre et des chicots pour leur nidification et, dans certains cas, pour leur alimentation (Angelstam et Mikusinski 1994; Martin et Eadie 1999; Imbeau et

Desrochers 2002a). Le diamètre est un facteur influençant la sélection des arbres par les oiseaux excavateurs, les arbres de gros calibre étant susceptibles de contenir une plus grande quantité d'insectes et de larves dont se nourrissent les pics (Gunn et Hagan III 2000; Nappi et al. 2003). De plus, certaines espèces de grande taille telle que le Grand Pic (*Dryocopus pileatus*) requièrent des chicots ou des arbres verts de grand diamètre pour nicher (Limoges et Tardif 1995). D'autre part, l'état de décomposition joue également un rôle important dans la sélection des substrats d'alimentation et de nidification, les arbres récemment morts étant utilisés lors de la quête alimentaire de certaines espèces telles que le Pic à dos rayé (*Picoides dorsalis*) et le Pic à dos noir (*Picoides arcticus*) (Imbeau et Desrochers 2002; Nappi et al 2003). Par contre, la fenêtre temporelle d'utilisation de ces arbres est relativement restreinte car ceux-ci ne constituent de bons substrats d'alimentation que dans les premières années suivant leur mort. L'étude de Farris et al. (2002), réalisée en Oregon et en Californie, montre en effet que les pics concentrent leurs recherches de nourriture alors que les larves de longicornes et de scolytes sont les plus abondantes, soit dans les premières années suivant la mort des arbres. Les chicots plus détériorés procurent pour leur part d'excellents substrats de nidification (Setterington et al. 2000). Plusieurs excavateurs primaires utilisent en effet des arbres au bois de cœur friable et au pourtour plus dur pour creuser leur nid (Adkins Giese et Cuthbert 2003); cela leur procure une certaine facilité lors de l'excavation tout en leur assurant une protection contre les prédateurs (Bunnell et al. 2002).

1.4 Importance de l'étude

Ces dernières années, le phénomène de la fragmentation en milieu forestier a reçu beaucoup d'attention, particulièrement dans les forêts feuillues et mixtes (Enoksson et al. 1995; Schmiegelow et al. 1997; Drapeau et al. 2000; Norton et al. 2000; Kurosawa et Askins 2003). Les effets que peuvent avoir la fragmentation et la perte d'habitat sont par contre moins bien connus en zone boréale de l'est de l'Amérique du Nord. Niemi et al. (1998) mentionnent en ce sens que les résultats d'études réalisées dans les forêts tempérées ne peuvent être directement appliqués aux forêts boréales puisque la dynamique forestière y est très différente. De plus, les travaux qui ont été menées portent très souvent sur les migrateurs

néotropicaux (Schmiegelow et al. 1997; Drolet et al. 1999; Drapeau et al. 2000; Norton et al. 2000; Hames et al. 2001). Imbeau et al. (2001) ont pourtant montré que les espèces résidentes des forêts boréales de l'est de l'Amérique du Nord et de Fenno-Scandinavie sont les plus sensibles à la foresterie industrielle. Ainsi, Imbeau et al. (2001) ont identifié les espèces les plus susceptibles d'être en conflit direct avec les activités d'aménagement forestier et parmi celles-ci figurent le Pic à dos rayé, le Pic à dos noir, le Grand Pic ainsi que la Mésange à tête brune. Il est par contre difficile d'évaluer les tendances des populations de chaque espèce ciblée dans la présente étude puisque cette information est quasi inexistante pour la forêt boréale de l'Est de l'Amérique du Nord.

D'autre part, le groupe des pics constitue un excellent indicateur de la disponibilité en arbres morts d'une forêt (Mannan et al. 1980). Ils jouent également un rôle essentiel au sein des écosystèmes forestiers en créant des cavités qui sont non seulement utilisées par une multitude d'espèces d'oiseaux mais également par plusieurs petits mammifères (Martin et Eadie 1999; Bevis et Martin 2002). La présence des utilisateurs secondaires de cavités à l'intérieur d'un peuplement forestier est donc intimement liée à celle des excavateurs primaires (Martin et Eadie 1999); la disparition de ces derniers pourrait alors avoir un impact négatif sur les espèces qui dépendent de leurs cavités pour survivre. Il est donc primordial de documenter la réaction de ces espèces dites « clés » en présence de conditions d'habitat sub-optimales afin d'être en mesure de préserver la biodiversité au sein des forêts aménagées.

1.5 Objectifs de l'étude

Ce mémoire, qui comporte deux chapitres, a comme objectif général de déterminer quels sont les effets de deux stratégies d'aménagement forestier en forêt boréale conifèrienne sur la distribution et le comportement de la guilde fonctionnelle des oiseaux excavateurs de cavités. Il est à noter que la comparaison de paysages soumis à divers types d'aménagement forestier, tel que présenté au chapitre 1, est rarissime dans la littérature existante, ce qui ajoute à l'unicité de la présente recherche. Il est également à noter que le chapitre 2 se veut une réplication géographique des études réalisées par Imbeau et Desrochers (2002a et 2002b)

qui ont eu lieu en zone de coupes agglomérées au Lac Saint-Jean. Les observations comportementales du Pic à dos rayé dans la présente étude ont par contre été réalisées à l'intérieur d'un système d'aménagement forestier très différent par rapport aux études antérieures, apportant ainsi une nuance intéressante et des connaissances complémentaires.

Les objectifs du premier chapitre sont donc de déterminer si des différences existent (1) quant aux attributs structuraux tels que les chicots entre les peuplements résiduels des coupes agglomérées et des coupes en mosaïque, (2) quant à la probabilité d'occurrence de huit espèces d'oiseaux excavateurs entre ces deux types d'habitats résiduels et (3) de déterminer si les variables à l'échelle du paysage influencent la probabilité d'occurrence de ces espèces.

En ce qui concerne le deuxième chapitre, les objectifs sont de déterminer (1) quelles sont les caractéristiques des arbres utilisés comme substrats d'alimentation par le Pic à dos rayé (*Picoides dorsalis*), (2) si la disponibilité des arbres récemment morts varie en fonction de la distance à la lisière bordant une coupe forestière et (3) si les patrons de déplacements du Pic à dos rayé, lors de sa quête alimentaire, sont influencés par la distance à la lisière.

EFFECTS OF SPATIAL CONFIGURATION OF CLEAR-CUTS ON THE ABUNDANCE AND OCCURRENCE OF PRIMARY CAVITY EXCAVATORS IN THE BOREAL FOREST OF NORTHWESTERN QUEBEC

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Abstract: Aggregated and dispersed clear-cutting patterns are two management strategies that differ greatly in terms of the amount and configuration of remaining habitat on the land base. The objectives of our study were to examine how the functional group of primary cavity excavators, that are strongly associated with late-successional attributes of stands (large live and dead trees), respond to (1) the amount of timber removal across the landscape, (2) the configuration of remnant forests and (3) the retention of late-successional features (large live trees, snags and logs) in remnant forests of landscapes harvested with aggregated and dispersed clear-cutting patterns. We sampled nine bird species using point count and playback methods. A total of 160 sites were sampled in both residual forest types. At the landscape level, the area of mature forest and the length of edges were significantly greater in the dispersed clear-cutting pattern than in the aggregated one. At the local scale, the basal area of live trees was significantly higher in larger forest patches of dispersed clear-cuts and the basal area of snags and logs was higher in riparian buffer strips and upland strips, respectively. Whereas the American Three-toed Woodpecker (*Picoides dorsalis*) and the Boreal Chickadee (*Poecile hudsonicus*) occurred more often in larger forest patches, large woodpeckers such as the Northern Flicker (*Colaptes auratus*) were significantly more abundant in linear strips of aggregated clear-cuts. Hierarchical logistic regression analysis shows that both local scale variables and landscape scale factors were important habitat features for all species. Finally, our study suggests that linear strips of aggregated clear-cuts should be permanently preserved from logging. Even though they may represent sub-optimal habitat for primary cavity excavators, they are nevertheless used by many of these species and they represent the last remaining fragments of mature and overmature forests in intensively managed landscapes. Thus, including large forest patches and connecting them to riparian linear tracts, in a permanent retention strategy, could improve the forest conditions for maintaining cavity excavating birds in managed forest landscapes.

Keywords: *primary cavity excavators, woodpeckers, weak cavity excavators, dispersed clear-cuts, aggregated clear-cuts*

Introduction

Boreal forest landscapes experience loss and fragmentation of mature habitats through natural disturbance regimes, that break up the continuity and generate heterogeneous landscapes (Harper et al. 2002). Hence, natural boreal forests are composed of a mosaic of forest cover types differing by their age, structure and composition (Bergeron et al. 2001, 2002, 2004). Forest-dwelling species inhabiting these ecosystems are thought to be well adapted to habitat loss and fragmentation since they have evolved along with large-scale disturbances (Schmiegelow et al. 1997; Drapeau et al. 2000; Imbeau et al. 2001). Therefore, they may be quite tolerant to habitat fragmentation, including the one created by timber harvesting. Concerns may nevertheless arise since discrepancies between natural and anthropogenic fragmentation of forest landscapes may be great, particularly with regards to the amount, size, shape and degree of isolation of remnant habitats (Harris 1984; Franklin and Forman 1987; Spies et al. 1994; De Long and Tanner 1996; Haila 1999; Kafka et al. 2001; Bergeron et al. 2002). On the other hand, landscape features, in conjuncture with local attributes, are known to affect species occurrence within habitat patches (Askins et al. 1987; Andrén 1994; Drapeau et al. 2000). Hence, forest remnants embedded in different landscape contexts may harbour different faunas even though local attributes are quite similar (Mönkkönen and Reunanen 1999).

In managed boreal forests, clear-cut patterns range from aggregated to dispersed cut blocks. Whereas, on the one hand, clear-cuts may be aggregated over larger spatial scales than natural disturbances (Belleau et al. in press), the dispersed checkerboard pattern, on the other hand, increases the length of edges, particularly when the amount of remnant forests reaches 50% (Franklin and Forman 1987). Moreover, habitat quality of remnant forests in managed landscapes is another component that may increase the contrast between managed and natural landscapes. The lack of structural attributes in harvested stands, particularly snags, may indeed result in a potential decrease in bird populations of cavity excavators and subsequently on secondary cavity users (birds and mammals), who are highly dependent on these attributes for reproducing and foraging (Angelstam and Mikusinski 1994; Martin and Eadie 1999).

Whereas an aggregated spatial distribution of clear-cuts may be more similar to natural disturbance patterns (OMNR 2001), its social acceptance may, however, be debatable. In this regard, dispersed clear-cutting has often been viewed as an alternative harvesting pattern (Haeussler and Kneeshaw 2003). However, its use is controversial. Potvin et al. (1999) showed that this strategy might better integrate the needs of multiple forest users than the aggregated pattern of clear-cuts but, on the other hand, this pattern of clear-cuts differs greatly from the one produced by wildfires (DeLong and Tanner 1996) and requires an extensive road network that increases artificial forest fragmentation. In recent years, regulations have switched from requiring aggregated to dispersed clear-cutting in Quebec's boreal forests. As different harvesting patterns are applied to forested landscapes, managers need to assess the effects of these changing conditions on wildlife populations.

In this paper, we compare the response of bird species associated with mature and overmature forests in cutover areas harvested with aggregated and dispersed clear-cutting patterns in the eastern boreal black spruce forest of northwestern Quebec, Canada. More specifically, we examine how the functional group of primary cavity excavators, that are strongly associated with late-successional attributes of stands (large live and dead trees), respond to (1) the amount of timber removal across the landscape, (2) the configuration of remnant forests and (3) the retention of late-successional features (large live trees, snags, logs) in remnant forests of landscapes harvested with aggregated or dispersed clear-cutting patterns.

Study area

The study area is located within the black spruce and feather moss bioclimatic zone (Robitaille and Saucier 1998) in the Nord-du-Québec region, near the community of Waswanipi (49° 12' to 50° 09' N and 75° 09' to 76° 37' W; Figure 1). Topography is generally flat with some scattered low elevation hills. Proglacial lake Ojibway has left glaciolacustrine deposits while depressions are filled by clay deposits (Gauthier et al. 2000). The mean temperature ranges from -2,5 to 0,0 °C and the mean total annual precipitation

ranges from 800 to 900 mm (Robitaille and Saucier 1998). Sampling sites were selected on public lands where logging activities have substantially modified the landscape (Figure 2). Dispersed and aggregated clear-cuts have spread throughout pristine forest mosaics, leaving at the regional scale (10 000 km^2) only relatively small blocks and linear strips as required by the Quebec Ministry of Natural Resources regulations (MRNQ 2003). Cut blocks adjacent to the sampling sites were harvested from 1987 to 2002. Dispersed clear-cut landscapes contained between 50-60% of remaining mature forests after the first harvesting pass. These remnant forests were distributed in patches of approximately 85-100 ha in size (MRNQ 2003). On the other hand, aggregated clear-cut landscapes generally contained between 20-25% of remnant mature forests. These remnants were mainly linear riparian strips or cut-block separators.

In each cutting pattern, 80 sampling sites were selected with regards to tree height, density and species composition of the forest cover. These remnant patches were composed of mature and overmature forests (> 70 years old) in which black spruce (*Picea mariana*) was the dominant tree species with sparsely distributed jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), larch (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Each sampling station was thus located within a relatively homogeneous forest cover type for either linear strips of aggregated clear-cuts or patch remnants of dispersed clear-cuts. Overall, 160 sampling stations provided extensive coverage of the study area.

Methods

Bird sampling

Nine cavity excavator birds species were sampled: Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*P. villosus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), American Three-toed Woodpecker (*P. dorsalis*), Black-backed Woodpecker (*P. arcticus*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Dryocopus pileatus*), Red-

breasted Nuthatch (*Sitta canadensis*) and Boreal Chickadee (*Poecile hudsonicus*). To avoid sampling the same individuals in two adjacent stations and given that woodpeckers have relatively large territories, all sampling points were at least 500 m apart. Bird censuses were conducted during the breeding season, which extended from late May to early July, in 2003 and 2004. Point counts were used to passively detect individuals by one observer. The day after recording point counts, another observer went back to the same stations and used the playback method to ensure that we detected the most species and individuals present as possible. Birds were classified with regards to detection distance (<75 m or >75 m). Whereas all detected songbirds were counted during sampling, in this paper we only consider birds detected within a 75 m radius. All sampling points were visited twice (for both playbacks and point counts) during the sampling period, once in the early morning (before 7h30) and once in the late morning (after 7h30). Sampling was carried out from 5h00 to 9h30, during days without rain and with low wind speed.

Local scale structural attribute sampling

Even though sampling site selection was made using criteria of homogeneity of the canopy cover in terms of tree height, density and species composition, key late-successional attributes vary from one sampling site to another. In each sampling station we thus sampled live trees, snags and downed logs. Stems were characterized according to their DBH (diameter at breast high), their deterioration state (Figure 2; Table 1; Imbeau and Desrochers 2002b) and their tree species. In large forest remnants, sampling was conducted along four transects oriented towards cardinal directions and each of them was 25 m long x 4 m wide, for a total of 400 m^2 per sampling point. In linear strips of aggregated clear-cuts, we sampled tree characteristics along three transects that crossed the entire width of forest strips. Transect width varied according to their length; for instance, when sampling riparian buffer strips, transects were generally 20 m long x 10 m wide (for a total area of 600 m^2) and when sampling upland strips, the transect width remained constant at four meters but the length varied according to the width of the strip (60 m to more than 100 m, for an area ranging from 720 m^2 to more than 1200 m^2).

Landscape variables

Landscape variables were divided into two categories: composition and configuration variables. The composition category included the area of mature forests and the area of clearings (cut areas and regenerating stands where trees were less than 7 m in height according to numerical forest maps) whereas configuration was measured using the length of edges and the distance to unlogged mature forests >500 ha. These variables were computed in three radii (75, 1000 and 2000 m) with the Arc GIS 9.0 program. We calculated the area of mature forest within a 75 m radius to characterize the amount of forest cover within our sampling stations.

Statistical analyses

We first assessed the differences in the amount, configuration and habitat quality of remnants for birds in the two cutting systems. For landscape features we used a U-test to assess whether these characteristics differed between the two cutting patterns. We predicted that the amount of mature forest and the length of edges should be greater in the dispersed clear-cuts landscape. For habitat quality, we compared late-successional attributes between remnant forest patches of dispersed clear-cuts and linear strips (riparian buffer strips and upland strips) from aggregated clear-cuts with a Kruskal-Wallis test. *Post hoc* comparisons of means between remnant habitats were performed using the Games-Howell test. This test was preferred over the Tukey HSD test since our sample sizes were unequal and the homoscedasticity assumption was not met in all cases. We predicted the basal area of snags and downed woody debris to be higher in linear strips (riparian buffer strips and upland strips) of aggregated clear-cuts than in the remnant forest patches of dispersed clear-cuts.

We then used the Fisher's Exact test to compare individual species' occurrence patterns between habitat types (forest patches vs linear strips) of the two cutting systems. The same procedure was also done for the total abundance of birds grouped by functional groups as follows: all woodpeckers, large excavators (Northern Flicker and Pileated

Woodpecker), small excavators (Hairy Woodpecker, Yellow-bellied Sapsucker, American Three-toed Woodpecker, Black-backed Woodpecker and Downy Woodpecker) and weak cavity excavators (Red-breasted Nuthatch and Boreal Chickadee). We predicted that all species but the Northern Flicker should occur more often in remnant forests of dispersed clear-cuts since they are all associated with mature forest. Conversely, given that the Northern Flicker is associated with open habitats, we predicted that its occurrence should be higher in linear strips of aggregated clear-cuts.

Whereas numerous studies have documented the importance, for animal population patterns and processes, of the landscape context within which habitats are embedded (McGarigal and McComb 1995; Jokimäki and Huhta 1996; Drapeau et al. 2000; Brotons et al. 2003), local habitat conditions within remnants also matter for organisms that depend on these habitats. To assess how local and landscape variables influenced the occurrence of cavity excavators, we performed hierarchical logistic regression models and used the Akaike's second-order information criterion (AIC_c) for model selection (Burnham and Anderson 2002). Before beginning the hierarchical procedure, we used the AIC_c method to pre-select the local vegetation variables considered most influential from a set of 15 models for each species that represented all possible combinations of the following four variables: 1) basal area of snags, 2) basal area of large live trees (DBH $\geq$20 cm), 3) basal area of deciduous live trees and 4) basal area of fallen trees. The first two variables were chosen since most of the cavity excavator bird species are dependant of those structural attributes for nesting and sometimes for foraging (Zarnowitz and Manuwal 1985; Villard and Beninger 1993; Villard 1994; Bevis and Martin 2002). Some of these birds can also forage or nest on downed woody debris or deciduous trees (Villard 1994; Harestad and Keisker 1989). We also pre-selected the composition and configuration landscape variables for each species with the AIC_c method among the following variables: 1) amount of mature forests, 2) amount of clear-cuts, 3) length of edges and 4) distance to unlogged mature forest > 500 ha. These variables were chosen since it is recognized, as previously mentioned, that the landscape context has a strong influence on the occurrence and abundance of forest-dwelling birds within habitat patches (McGarigal and McComb 1995; Jokimäki and Huhta 1996; Drapeau et

al. 2000; Brotons et al. 2003). Moreover, the length of edges and the distance to unlogged mature forests are two indicators of the degree of fragmentation of the landscape.

The first step of the hierarchical approach for the logistic regression models consisted in the construction of the null model, which simply contained the intercept. Then, we developed a model that examines how birds are sensitive to the amount of mature forests at the stand scale (within the 75 m radius). This step was necessary before examining the contribution of local structural features in species occurrence, since the percentage of mature forests at this spatial scale is quite different between the remnant shapes generated by the two cutting patterns. It was thus important to control for the local effects of habitat amount. The third step of the hierarchical approach consisted in building the "local" model that included the area of mature forest at the local scale and local vegetation attributes that were previously selected. In a fourth step, we then added the variables that depicted the amount and composition of the surrounding landscape and, in a final step, we added the landscape variables that describe the spatial configuration of remnant habitats. This procedure allowed us to assess whether the addition of a new group of variables enhanced the overall strength of evidence of the models. When several models competed for the first rank, we used the multi-model inference approach (model-averaging), which allowed us to identify the most influential variables from the entire set of models that contained these variables instead of relying solely on one "best" model (Burnham and Anderson 2002). This hierarchical approach of model construction was repeated with Poisson regression models for functional groups of birds (all woodpeckers, large woodpeckers, small woodpeckers and weak excavators) to assess whether the overall abundance was influenced by landscape variables. Prior to these analyses, we ensured that the assumptions were met and that the data showed an appropriate distribution.

We expected single species and functional groups to be positively influenced by the basal area of snags at the local scale and by the area of mature forests at the landscape level.

Results

Overall landscape patterns

As expected, the area of mature forests was significantly greater in the remnant forest patches of the dispersed clear-cutting pattern (56 %) compared with linear forest strips of aggregated clear-cuts (22-25%; Table 2). The area of clearings was also significantly different between the two landscapes, reaching 29-32% and 60-65% in dispersed and aggregated clear-cutting patterns, respectively (Table 2). The length of edges was significantly greater in the dispersed pattern of clear-cuts within the 2000 m radius but there was no significant difference when considering this variable in the 1000 m radius. The distance between sampling stations and large extent of mature forests was also significantly greater in dispersed clear-cuts landscape compared with the aggregated one. At the local scale, c.a. in the 75 m radius, the amount of mature forests was higher in dispersed clear-cuts (98%) compared with the aggregated clear-cuts (55%; Table 2) and the amount of clearings was, conversely, greater in aggregated (39%) than in dispersed (<1%) clear-cuts landscapes. At this scale, the length of edges was also significantly greater in the aggregated clear-cutting pattern (Table 2).

Comparisons between remnants in dispersed and aggregated clear-cuts

We characterized a total of 7 889 stems in large forest patches and 15 576 stems in linear strips. Overall, the basal area of all stems (regardless of deterioration stage) was similar among the three habitats, indicating we were in the presence of the same forest cover type prior to disturbance. The basal area of live trees was significantly higher in larger forest patches while the basal area of snags and fallen trees was higher in riparian buffer strips and upland strips, respectively (Table 3). Live trees basal area (classes 1 and 2), which represented the majority of sampled stems, was higher in larger forest remnants. The basal area of dying trees (class 3) was similar among habitats whereas recently dead trees (class 4), was slightly greater in linear strips, but the *post hoc* test did not detect differences between groups. The basal area of snags at an intermediate deterioration stage (class 5) was

significantly higher in linear strips than in larger forest remnants. Old snags (class 6) were more important in larger forest remnants. The basal area of very old snags (class 7) and of stumps (class 8) was higher in buffer strips but the Games-Howell *post hoc* test did not detect a significant difference among habitats. Thus, there seems to be a trend towards more snags in early decay stage in linear remnants than in large remnant patches. The basal area of recently fallen trees (class 9) and of very old logs (classes 12 and 13) was similar among habitats whereas intermediate logs (class 10) and old logs (class 11) were significantly more abundant in upland strips. When looking at stems DBH, the basal area of live trees larger or equal to 10, 15 and 20 cm was greater in larger forest remnants even though the Kruskal-Wallis test for the latter category was not significant. The basal area of snags larger or equal to 10, 15 and 20 cm was higher in riparian buffer strips but the *post hoc* test did not detect significant differences between groups for the latter category. Finally, the basal area of fallen trees larger or equal to 10, 15 and 20 cm was higher in upland strips even though the *post hoc* test did not detect significant differences for the two latter categories. Overall, despite the differences between upland and riparian buffer strips in terms of snags and logs, the proportion of these structural attributes was still higher in both linear habitats than in larger forest patches.

Influence of habitat types on the occurrence of primary cavity excavators

Figure 3 and Table 4 summarize the relationship between bird specie's occurrences and habitat type (larger forest patches vs linear strips). The Hairy Woodpecker and the Northern Flicker were both detected more often in linear strips whereas the American Three-toed Woodpecker and the Boreal Chickadee were more often detected in larger forest remnants. When grouping birds into functional groups, the Fisher's exact test revealed that the occurrence of all woodpeckers and of small excavators was similar between the two habitats. The occurrence of large woodpeckers, mainly represented by the Northern Flicker, was significantly higher in linear strips of aggregated clear-cuts. Finally weak cavity excavators occurred more often in larger forest remnants of the dispersed clear-cuts pattern than in linear strips of aggregated cleat-cuts (Figure 3 and Table 4).

Local and landscape variables influencing the bird occurrence and abundance

Model selection with the AIC_c approach for individual species and for functional groups of species are shown in Tables 5 and 6, respectively. For either individual species or species groups the model selection approach based on AIC_c scores showed that many models shared high strength of evidence and that these models included both local and landscape scale habitat variables. Hence, given that we were unable to choose one single best model, we used the multimodel inference approach (model-averaging) to extract the most important variables (Tables 7 and 8). First, local scale variables were important habitat features for 5 out of 7 species and models that included either the amount of mature forest within 75 m or local vegetation variables were also considered the best model according with the AIC_c approach in 5 of the 7 species (Table 5), and in 2 out of 4 functional groups (Table 6). Landscape scale factors were also considered important since these variables came out as important determinants for all species (Table 5) and for 3 out of 4 functional groups (Table 6). Within the fragmentation gradient generated by these two cutting patterns, the landscape configuration of habitat remnants was important for all species except the Yellow-bellied Sapsucker whereas this feature was less important for models that included functional groups of species as the response variable with 2 of the 4 functional groups (Table 6). Given that throughout our data set the "best" model has many competitors for the top rank, multimodel inferences used all the information available from the entire set of models to sort out the most influential variables. Multimodel inference analyses show that Yellow-bellied Sapsucker, American Three-toed Woodpecker and Red-breasted Nuthatch responded more to local scale attributes whereas the Black-backed Woodpecker, the Boreal Chickadee and the Northern Flicker were more influenced by landscape variables that depicted the habitat composition of the surroundings (Table 7). The Northern Flicker was the only species where a configuration variable (distance to unlogged mature forests) affected its occurrence. When looking at functional groups, the "all woodpeckers group" was affected by local and configuration landscape attributes whereas the abundance of small woodpeckers and of WCE were only influenced by local attributes (Table 8). For small excavators, this is a bit surprising given that the occurrence of some species was affected by landscape composition variables. One possible explanation is that American Three-toed Woodpecker, which was influenced by the

basal area of woody debris (Table 6), was the species that occurred the most often within this group and was thus likely to have a greater influence. For large excavators, the multimodel inference approach did not bring additional information about habitat attributes that may influence their abundance. But since the large woodpeckers group was composed almost exclusively of Northern Flicker, the Pileated Woodpecker being practically absent from the study area, we shall rely mainly on results obtained from the multimodel inference approach for the Northern Flicker as an individual species.

Discussion

Overall bird responses to cutting patterns

Our prediction that all species but the Northern Flicker should occur more often in larger forest remnant patches than in linear strips of aggregated clear-cuts was partly corroborated. Indeed, the American Three-toed Woodpecker and the Boreal Chickadee were both more abundant in larger forest patches. These species are known to be associated with overmature forests (Conseil canadien des ministres des forêts 1997; Imbeau et al. 1999; Imbeau et al. 2001). Hence, their higher abundance in the landscape showing the highest amount of mature and old-growth forests is not surprising. Our results are also in accordance with those of other studies that showed that the occurrence of American Three-toed woodpeckers is positively correlated with the amount of undisturbed mature forests (Imbeau and Desrochers 2002a). In northern Finland, Virkkala (1987) showed that the density of Three-toed woodpeckers was significantly lower in fragmented than in contiguous forests. Imbeau and Desrochers (2002a) also showed that the frequency of occurrence of American Three-toed Woodpecker was three times higher in continuous forest than in linear strips of aggregated clear-cuts while the forest cover was about four times higher in continuous forest. In our study area, the frequency of occurrence of this forest-dwelling species was three times higher in dispersed clear-cuts landscapes than in aggregated clear-cuts whereas the overall amount of mature forests was twice as high in dispersed than in aggregated clear-cuts. Our results thus suggest that the reduction of mature forest habitat in these cutting systems has an

effect on populations that is superior to the one induced by pure habitat loss (a one to one population reduction with regards to loss of habitat). In fact, the effect of configuration of habitat patches on the bird occurrence seems more important in our study compared with the one of Imbeau and Desrochers (2002a). Hence, the American Three-toed Woodpecker population in our study area seems to respond in a non-linear fashion (*sensu* Andrén 1994) to the amount of mature forests in this landscape when it falls from 56 to 22%. On the other hand, the hierarchical logistic regression models and the AIC_c results for the American Three-toed Woodpecker and the Boreal Chickadee were also negatively associated with the amount of clear-cuts within a radius of 2 km, emphasizing the avoidance, by these species, of highly fragmented landscapes.

The Hairy Woodpecker was more abundant in linear strips of aggregated clear-cuts than in larger forest remnants of dispersed clear-cuts. This species inhabits mature (Lemieux 1995) and recently burned forests (Villard and Beninger 1993, Murphy and Lehnhausen 1998), but occurs also in smaller and more open woodlands while nesting in a dead part of a live tree (Harestad et Keisker 1989). Concerning the Hairy Woodpecker, the presence of trembling aspens left standing within clear-cuts at the edge of the remnant forests could have attracted individuals since those trees represent good nesting substrates (Harestad and Keisker 1989; CG pers. obs.). The overall low sample size (eight individuals) may however be insufficient to allow us to generate any valid conclusions about the habitat preference of the Hairy Woodpecker.

As predicted, the Northern Flicker was significantly more abundant in aggregated than in dispersed clear-cuts. This ground-foraging species requires open habitat to carry out its foraging activities and large snags for nesting (Ehrlich et al. 1988; Harestad and Keisker 1989; Bevis and Martin 2002), conditions that occur in aggregated cutting patterns. The hierarchical logistic regression models and the AIC_c approach showed that the amount of clear-cuts at the landscape scale positively influenced its occurrence, which is consistent with other studies (Setterington et al. 2000; Bevis and Martin 2002). The Northern Flicker was positively associated with the proximity of large tracks of mature forests, which is counterintuitive to this species' common use of open habitats. However, this may be

explained by the fact that sampling points located in the aggregated clear-cuts landscape were, on average, closer to large tracks of mature forests than the ones located in dispersed clear-cuts landscape, where the alternance of cut and uncut blocks reduces the occurrence of large extent of mature forests.

For functional groups, contrasts between aggregated and dispersed cutting patterns where mainly driven by the higher abundance of weak excavators in larger forest remnants and higher abundance of large excavators, namely Northern flickers, in aggregated clear-cuts.

Hence, bird assemblages in both cutting patterns differed slightly even though the overall bird abundance does not differ. Aggregated clear-cuts represent a better environment for large woodpeckers such as the Northern Flicker, whereas dispersed clear-cuts appear to be a better habitat for small woodpeckers and WCE. This difference in the composition of primary excavators may have direct consequences on secondary cavity users inhabiting those fragmented forests. Indeed, the use of a forest patch by secondary cavity users is constrained by cavities produced by primary excavators, these cavities thus representing a critical resource (Martin and Eadie 1999). Our results suggest that the availability of large cavities may be higher in linear strips because of the higher occurrence of the Northern Flicker in this habitat. Consequently, large secondary cavity nesters may occur in these highly fragmented landscapes, as long as they can find breeding conditions either within cut blocks or at the edge of remnant habitats. Conversely, a greater availability of small cavities may be found in larger forest patches of dispersed clear-cuts. Secondary cavity nesters that use small cavities may thus do better in larger forest patches than in linear strips.

What attributes are driving the habitat selection of primary cavity excavators?

It is recognized that the distribution patterns of species are affected by processes occurring at the patch level along with those occurring at a larger scale, within the matrix (Donovan et al. 1997; Villard 1998; Drapeau et al. 2000). The species occurrence and dynamics within fragments may then vary as the matrix surrounding forest fragments change (Wiens 1994; Mönkkönen and Reunanen 1999). However, in boreal forests, it is well

recognized that the landscape composition affects more importantly the abundance and distribution of forest-dwelling species than its configuration (Rosenberg and Raphael 1986; Hejl 1992; Drapeau et al. 2000), yet species can also be impacted by the spatial pattern of remaining habitats. In our study area where large-scale timber harvesting occurred, models that included landscape composition vs landscape configuration variables all had high strength of evidence. Hence, configuration variables came out as often as landscape composition variables for all species but most particularly for the Northern Flicker, for which multi-model inference analyses identified configuration as an influential variable. Models that considered configuration features were thus competing with the other models suggesting that the forest-dwelling species under study were indeed not only affected by the loss of mature forests in highly harvested landscapes but also by the spatial configuration of cutting patterns and remnant habitats.

Habitat quality in remnant habitats of aggregated and dispersed cutting patterns

Mascarúa-López et al. (2006) suggest that there exists a high level of structural similarity between continuous forests, larger forest remnants, riparian buffer strips and upland strips but that dead trees could discriminate these three habitats from one another. In our study, dead trees and fallen trees basal areas were indeed higher in linear strips of aggregated clear-cuts than in larger forest patches of dispersed clear-cuts, suggesting that the shape and width of forest remnants are factors that can greatly contribute to structural changes of the forest. The basal area of live trees was higher in larger forest patches than in linear strips whereas snags and logs were more numerous in riparian buffer strips and upland strips, respectively. Mascarúa-López (2005) obtained similar results in remnant habitats of harvested landscapes in northwestern Quebec. In fact, she showed that riparian buffer strips and upland strips were more sensitive to harsh conditions generated by adjacent clearings than were forest interior conditions of larger forest patches. Elevated soil temperatures and changes in plant water use efficiency (Chen et al. 1993; Kapos et al. 1993) are well established consequences of the increased exposure near newly created edges and can have led to an increase of the mortality rate of trees. Stronger and more turbulent winds can also

have raised the number of blown down trees in these shredded linear forests (Franklin and Forman 1987; Esseen 1993; Darveau et al. 1995).

The abundance of snags and logs came out as an influential factor for most bird species. Hence, the increased abundance of dead wood in linear strips of aggregated clear-cuts is a factor that may explain the persistence of forest-dwelling species even though the amount of mature forest cover is far less than in larger forest patches of dispersed clear-cuts. Thus, habitat quality in these linear remnants does matter in respect to snag and log densities.

Management implications

In the short term, the dispersed pattern of clear-cuts may be more appropriate for the maintenance of forest-dwelling species and, more generally, for the maintenance of biodiversity in managed forests than the aggregated pattern of clear-cuts. In the long term, however, larger forest patches will be harvested as the adjacent regenerating forest will reach three meters in height (MRNQ 2003), leaving mature and old-growth forests only in riparian buffer strips like in the aggregated clear-cuts landscapes. Hence, the current distribution patterns of forest-dwelling birds in our aggregated clear-cuts may provide a forecast of what is likely to occur in dispersed clear-cuts when the second harvesting is conducted in these landscapes.

The negative impacts of large-scale openings in aggregated clear-cuts was less than expected given the strong reduction in the amount of overmature forest and the linear shape (high proportion of edge habitat) of the remnants. For snag users, such as the forest-dwelling specialists under study, this overall loss of mature forest habitat could however be offset by the maintenance, in these linear strips, of the variety of snag DBH and decay states that are found in larger forest patches. The loss of large extent of mature forest could also be offset by a higher prevalence of high quality foraging substrates, such as recently dead trees, in linear buffer strips and edge habitat (Gagné, chapter 2). A challenging issue in these narrow forest strips will be to ensure that dynamics of recruitment of wildlife trees be maintained through

permanent and constant supply of snags for nesting and foraging woodpeckers. To do so, such remnants should form the basis of permanent retention of older forests in managed landscapes. Presently, the Quebec forest regulations do not protect on a permanent basis these linear remnants. Upland strips are included in the annual allowable cut (AAC) and must be harvested when regenerating harvested stands reach three meters in height whereas riparian strips can be partly harvested. Moreover, linear habitats are subject to edge effects (Mascarúa-López et al. 2006) that can alter their capacity to provide forest conditions similar to those offered by unfragmented tracts of overmature forests. Hence, including large patches and connecting them to riparian linear tracts in a permanent retention strategy could improve the forest conditions for maintaining biodiversity in managed forest landscapes.

Despite that all primary cavity excavators were present in shredded forests of aggregated clear-cuts, this landscape nevertheless remained a sub-optimal habitat for the majority of species, except perhaps the Northern Flicker. In fact, our results suggest that cavity excavators are quite tolerant to habitat loss and fragmentation and they respond both to the extent of habitat loss and to the configuration of the remnant fragments. Hence, if we aim to manage the forest while preserving biodiversity, forest managers and stakeholders should consider other, more innovative, cutting patterns than aggregated clear-cuts. For instance, one alternative that has been extensively discussed over recent years is to model cutting patterns on the natural disturbance regime that takes place in a given area (Galindo-Leal and Bunnell 1995; Leduc et al. 2000). In boreal forests, for instance, the maintenance of a higher proportion of overmature stands in the managed landscape could come from increasing the use of partial cutting practices that preserve stand structure of uneven-aged and old-growth forest stands (Bergeron et al. 2001, 2004; Gauthier et al. 2001; Harper et al. 2002). This could considerably increase the amount of overmature forests remaining in managed landscapes and thus, maintain populations of primary excavators at levels that may reach the population levels found in naturally disturbed forests.

List of figures

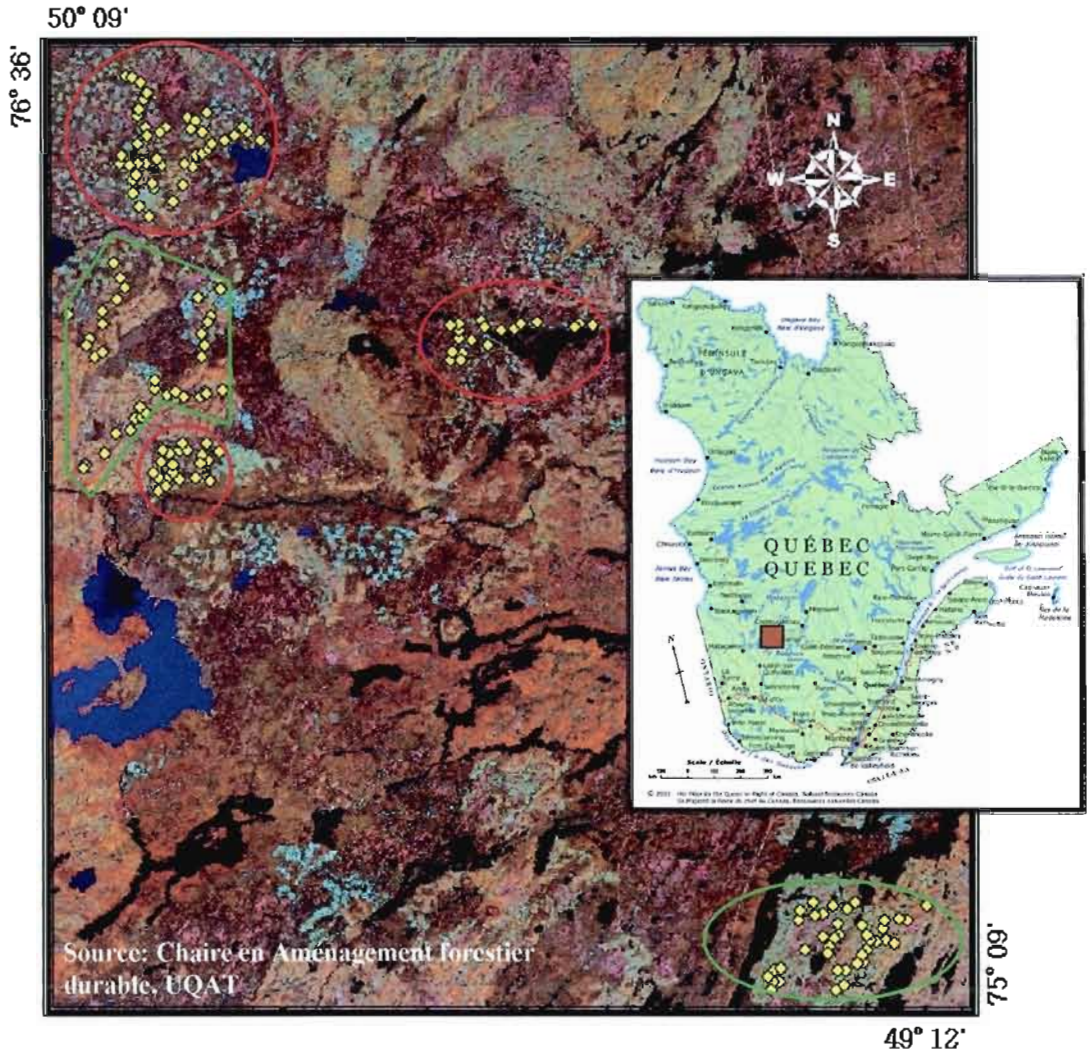
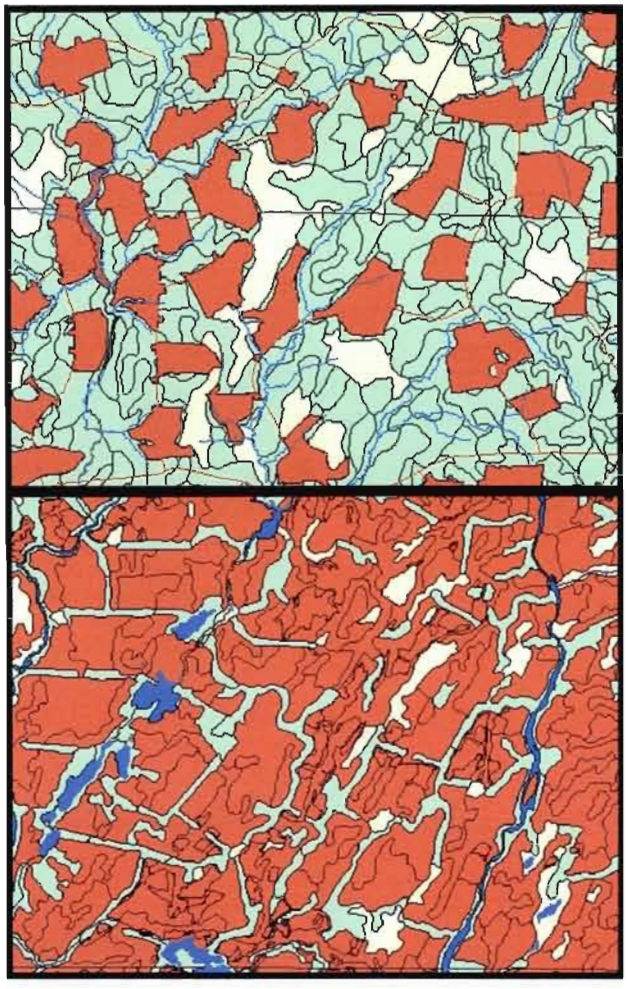


Figure 1. Gagné et al.



Legend

Dispersed and aggregated cutting patterns

- Cutover areas and forest stands < 7 m of heigth
- Partial windthrow
- Forest peat bog
- Water
- Forest stands > 7 m of heigth

Figure 2. Gagné et al.

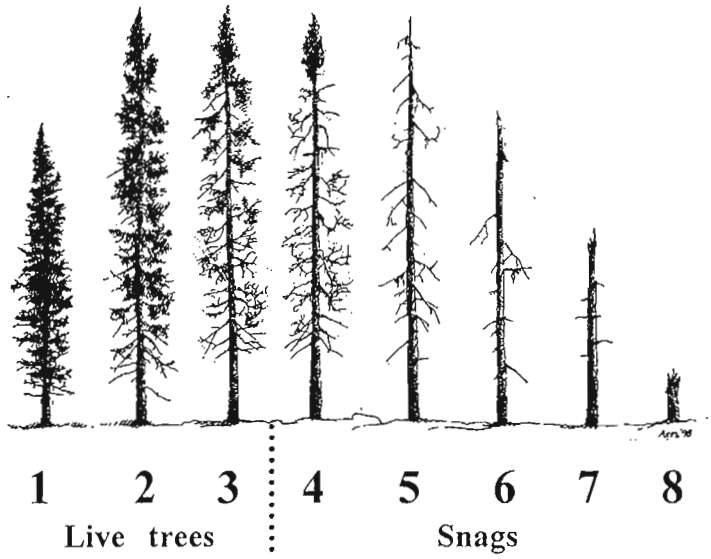


Figure 3. Gagné et al.

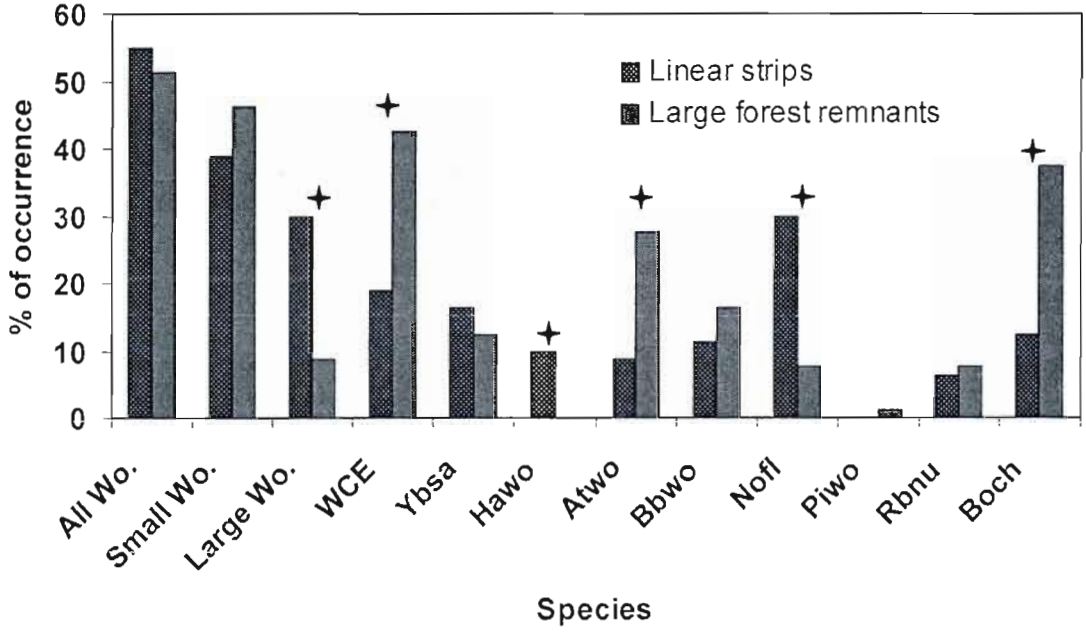


Figure 4. Gagné et al.

Table 1. Characteristics of live trees, snags and downed logs according to their deterioration state, Nord-du-Québec, Quebec, Canada, 2003-2004.

Deterioration class		Tree characteristics
Live trees		
1	(healthy tree)	Alive and healthy, ≥95% foliage, no signs of deterioration
2	(healthy tree)	Declining, remaining foliage between ≥20% and <95%, senescent tree
3	(dying tree)	Dying, <20% foliage remaining
Snags		
4	(recently dead tree)	Recently dead, hard wood, firm bark cover, dead foliage and small twigs still remaining
5	(intermediate snag)	Hard wood, firm bark cover, no dead foliage, no small twigs
6	(old snag)	Hard wood, loose bark cover, broken top, height still more than 50% of what is observed on trees with same DBH
7	(very old snag)	Soft, decomposed wood, broken top with height less than 50% of what is observed on trees with same DBH
8	(stump)	Stump, height <2 m
Downed logs		
9	(recently fallen tree)	Recently fallen, hard wood, firm bark cover and small twigs still remaining
10	(intermediate log)	Hard wood, no dead foliage, no small twigs, bark cover still remaining but more easily removable
11	(old log)	Wood still hard but less than the previous classes, loose bark cover, can be partially covered by mosses
12	(very old log)	Soft, decomposed wood, bark is almost absent, most often covered by mosses
13	(very old log)	Wood is partly or entirely integrated to organic matter

Table 2. Composition and configuration landscape features in dispersed and aggregated clear-cuts of black spruce forests in northwestern Quebec, Canada, 2003-2005.

	Dispersed clear-cuts				Aggregated clear-cuts				
Variables[a]	**Mean**	**%**	**SE**	**%**	**Mean**	**%**	**SE**	**%**	**p**[b,c]
Local composition (75 m radius)									
Area of mature forests	17 258	97.66	1 519	8.60	9 736	55.09	4 387	24.82	**0.000**
Area of clearings	4	0.02	39	0.22	6 908	39.09	3 204	18.13	**0.000**
Landscape composition									
Area of mature forests (1000 m radius)	1 775 898	56.53	327 157	10.41	691 143	22.00	336 378	10.71	**0.000**
Area of mature forests (2000 m radius)	7 061 215	56.19	1 061 165	8.44	3 106 937	24.72	1 616 292	12.86	**0.000**
Area of clearings (1000 m radius)	1 008 887	32.11	379 263	12.07	2 045 563	65.11	346 602	11.03	**0.000**
Area of clearings (2000 m radius)	3 661 778	29.14	1 281 508	10.20	7 522 582	59.86	1 418 321	11.29	**0.000**
Local configuration (75 m radius)									
Length of edges	13	-	41	-	201	-	89	-	**0.000**
Landscape configuration									
Length of edges (1000 m radius)	13 092	-	3 103	-	12 386	-	3 903	-	0.153
Length of edges (2000 m radius)	49 867	-	9 651	-	46 490	-	11 072	-	**0.014**
Distance to unlogged mature forests >500 ha	6 924	-	4 195	-	4 393	-	2 812	-	**0.000**

[a] Areas are expressed in square meters and the lengths and distance are expressed in meters.

[b] The p-value following the U-test.

[c] Resutls in bold are significant with the sequential Bonferroni correction.

Table 3. Basal area of live trees, snags and logs according to their deterioration state and DBH in linear strips (upland and riparian buffer strip) of aggregated clear-cuts and in large forest remnant patches of dispersed clear-cutting patterns, in black spruce forests of northwestern Quebec, Canada, 2003-2004.

	Upland strips[c]		Riparian buffer strips[c]		Large forest remnants[c]			
	Mean	SE	Mean	SE	Mean	SE	H	p[d]
Live trees	15.9[a]	0.9	16.3[a]	1.1	22.2[b]	0.9	23.7	**0.000**
Deciduous trees	0.7*	0.2	0.6*	0.3	0.4*	0.1	8.8	**0.012**
Snags	8.4	0.4	9.0[a]	0.5	7.2[b]	0.5	13.1	**0.001**
Downed logs	10.9[a]	0.9	8.2[b]	0.7	7.7[b]	0.7	10.5	**0.005**
All stems	35.2	1.3	33.5	1.4	37.1	1.3	4.4	0.111
Deterioration state								
Live trees								
1-2	11.0[a]	0.7	11.1[a]	1.0	18.6[b]	0.9	39.9	**0.000**
3	4.9	0.5	5.2	0.8	3.6	0.3	5.9	0.053
Snags								
4	1.6*	0.2	1.6*	0.1	1.4*	0.2	6.1	**0.047**
5	1.5[a]	0.1	1.6[a]	0.2	1.0[b]	0.1	16.0	**0.000**
6	0.7	0.1	0.4[a]	0.1	0.8[b]	0.1	6.4	**0.040**
7	1.7*	0.2	1.8*	0.2	1.4*	0.2	10.1	**0.006**
8	2.8*	0.3	3.5*	0.3	2.6*	0.2	7.2	**0.028**
Fallen trees								
9	0.7	0.1	0.5	0.1	0.7	0.1	3.1	0.217
10	4.1[a]	0.3	2.7[b]	0.3	2.3[b]	0.2	23.4	**0.000**
11	4.4[a]	0.5	3.9	0.5	2.6[b]	0.3	13.4	**0.001**
12-13	1.7	0.2	1.1	0.2	2.1	0.3	3.1	0.214
Diameter classes								
Live trees								
≥10 cm	14.2[a]	1.0	14.0[a]	1.1	20.1[b]	1.0	19.7	**0.000**
≥15 cm	10.7[a]	0.9	10.3[a]	1.0	14.9[b]	1.0	11.2	**0.004**
≥20 cm	5.5	0.6	5.9	0.8	8.2	0.8	2.8	0.246
Snags								
≥10 cm	7.9	0.5	8.5[a]	0.5	6.5[b]	0.5	15.2	**0.001**

Table 3. (continued)

	Upland strips[c]		Riparian buffer strips[c]		Large forest remnants[c]			
	Mean	SE	Mean	SE	Mean	SE	*H*	p[d]
≥15 cm	6.3	0.5	7.0[a]	0.5	5.1[b]	0.5	14.2	**0.001**
≥20 cm	4.0*	0.5	4.2*	0.4	3.1*	0.4	12.5	**0.002**
Fallen trees								
≥10 cm	9.8[a]	0.8	7.3	0.7	6.8[b]	0.6	10.2	**0.006**
≥15 cm	6.7*	0.7	4.9*	0.5	4.7*	0.5	8.3	**0.016**
≥20 cm	3.2*	0.5	2.1*	0.4	2.3*	0.4	7.4	**0.024**

[a,b] Values with distinct letters are significantly different according to the Games-Howell *post hoc* test.

* The *post hoc* test was unable to detect any differences between groups.

[c] Upland strips, n = 38; Buffer strips, n = 42 and Large forest remnants, n = 80.

[d] Results in bold are significant at the 0.05 level.

Table 4. Occurrence of primary cavity excavators and of birds grouped in functional groups (number of sampling stations where at least one species of a group was detected) in remnant forests of dispersed and aggregated clear-cuts in black spruce forests of northwestern Quebec, Canada, 2003-2004. Values represent the number of sampling stations where birds were detected and numbers in parentheses represent the probability of occurrence (%) of species and functional groups.

	Large forest remnants N=80	Linear strips N=80	Overall N=160
Species			
Hairy Woodpecker	0 (0.0)	8 (10.0)	8 (5.0)
Yellow-bellied Sapsucker	10 (12.5)	13 (16.3)	23 (14.4)
American Three-toed Woodpecker	22 (27.5)	7 (8.8)	29 (18.1)
Black-backed Woodpecker	13 (16.3)	9 (11.3)	22 (13.8)
Northern Flicker	6 (7.5)	24 (30.0)	30 (18.8)
Boreal Chickadee	30 (37.5)	10 (12.5)	40 (25.0)
Red-breasted Nuthatch	6 (7.5)	5 (6.3)	11 (6.9)
Pileated Woodpecker	1 (1.3)	0 (0.0)	1 (0.6)
Functional groups			
All Woodpeckers	41 (51.3)	44 (55.0)	85 (53.1)
Large Excavators	7 (8.8)	24 (30.0)	31 (19.4)
Small Excavators	37 (46.3)	31 (38.8)	68 (42.5)
Weak cavity excavators	34 (42.5)	15 (18.8)	49 (30.6)

Table 5. Model selection with the AIC_c approach for the occurrence of primary cavity excavators, in black spruce forests of northwestern Quebec, Canada, 2003-2004.

Model	Variable	-2ll	k	AIC_c	ΔAIC_c
YBSA					
Null	---	131.8	1	133.8	6.2
Local	fo_75	131.2	2	135.3	7.6
*Local attributes	fo_75 + lt_20 + snags + logs	117.3	5	127.7	0.0
[a]Composition landscape	fo_75 + lt_20 + snags + logs + cut_2000	116.4	6	128.9	1.3
Configuration landscape	fo_75 + lt_20 + snags + logs + cut_2000 - edge_2000	116.1	7	130.8	3.2
HAWO					
Null	---	63.5	1	65.5	9.0
Local	-fo_75	56.8	2	60.8	4.3
Local attributes	- fo_75 + logs + deci	50.7	4	58.9	2.5
*Composition landscape	- fo_75 +logs + deci + cut_2000	46.1	5	56.5	0.0
[a]Configuration landscape	- fo_75 + logs + deci + cut_2000 + edge_1000	44.3	6	56.9	0.4
ATWO					
Null	---	151.5	1	153.5	12.2
[a]Local	fo_75	137.8	2	141.9	0.6
[a]Local attributes	fo_75 - lt_20 + logs	133.2	4	141.4	0.1
*Composition landscape	fo_75 – lt_20 + logs - cut_2000	130.9	5	141.3	0.0
[a]Configuration landscape	fo_75 – lt_20 + logs - cut_2000 + edge_2000	130.3	6	142.9	1.5
BBWO					
[a]Null	---	128.1	1	130.1	0.8
*Local	Fo_75	125.3	2	129.4	0.0
[b]Local attributes	fo_75 - snags - deci	124.3	4	132.6	3.2
[a]Composition landscape	fo_75 - snags - deci + fo_1000 + cut_1000	117.5	6	130.0	0.7
[a]Configuration landscape	fo_75 - snags - deci + fo_1000 + cut_1000 - edge_2000	116.1	7	130.8	1.5

Table 5. (continued)

Model	Variable	-2ll	k	AICc	ΔAICc
NOFL					
Null	---	154.4	1	156.4	7.4
Local	- fo_75	151.2	2	155.3	6.3
Local attributes	- fo_75 - lt_20 + deci	148.3	4	156.5	7.5
Composition landscape	- fo_75 - lt_20 + deci + cut_1000	140.7	5	151.1	2.1
*Configuration landscape	- fo_75 - lt_20 + deci + cut_1000 - dist	136.5	6	149.0	0.0
RBNU					
Null	---	80.1	1	82.1	4.4
Local	fo_75	79.8	2	83.9	6.2
*Local attributes	- fo_75 + lt_20 – snags + deci	67.3	5	77.7	0.0
[a]Composition landscape	fo_75 + lt_20 – snags + deci + cut_1000	66.1	6	78.6	1.0
[a]Configuration landscape	fo_75 + lt_20 - snags + deci + cut_1000 + edge_2000	64.7	7	79.4	1.7
BOCH					
Null	---	179.9	1	181.9	12.7
*Local	fo_75	165.2	2	169.3	0.0
Local attributes	fo_75 + lt_20 - snags	163.9	4	172.1	2.9
[a]Composition landscape	fo_75 + lt_20 – snags - cut_2000	160.3	5	170.7	1.4
[a]Configuration landscape	fo_75 + lt_20 -- snags - cut_2000 - lis_1000	158.2	6	170.7	1.4

* Best models according to the AIC_c approach.

[a] Competing models with a $\Delta AIC_c < 2$.

[b] The local model does not fit according to the Hosmer and Lemeshow criterion but we nevertheless kept it as an indication.

Table 6. Model selection with the AIC_c approach for the abundance of primary cavity excavators in functional groups, in black spruce forests of the northwestern Quebec, Canada, 2003-2004.

Model	Variable	-2ll	k	AIC_c	ΔAIC_c
All woodpeckers					
Local	fo_75	196.9	2	201.0	7.6
[a]Local attributes	fo_75 + lt_20 + logs + deci	184.2	5	194.6	1.2
Composition landscape	fo_75 + lt_20 + logs + deci + fo_1000 + cut_1000	183.1	7	197.9	4.4
*Configuration landscape	fo_75 + lt_20 + logs + deci + fo_1000 + cut_1000 - edge_2000 - dist	174.2	9	193.4	0.0
Large woodpeckers					
Local	- fo_75	111.8	2	115.9	2.1
Local attributes	- fo_75 - lt_20 + logs + deci	106.6	5	117.0	3.2
[a]Composition landscape	fo_75 - lt_20 + logs + deci + fo_1000 + cut_1000	100.5	7	115.3	1.5
*Configuration landscape	fo_75 - lt_20 + logs + deci + fo_1000 + cut_1000 - edge_2000 - dist	94.6	9	113.8	0.0
Small woodpeckers					
Local	fo_75	178.1	2	182.2	4.8
*Local attributes	fo_75 + lt_20 + logs + deci	167.1	5	177.5	0.0
[a]Composition landscape	fo_75 + lt_20 + logs + deci + fo_2000	166.9	6	179.4	2.0
Configuration landscape	fo_75 + lt_20 + logs + deci + fo_2000 - edge_2000 - dist	162.7	8	179.6	2.2
Weak cavity excavators					
*Local	fo_75	132.1	2	136.2	0.0
[a]Local attributes	fo_75 + lt_20 - snags	129.8	4	138.0	1.8
Composition landscape	fo_75 + lt_20 - snags + fo_2000 - cut_2000	128.5	6	141.1	4.9
Configuration landscape	fo_75 + lt_20 - snags + fo_2000 - cut_2000 - edge_2000	128.3	7	143.1	6.9

* Best models according to the AIC_c approach.

[a] Competing models with a $\Delta AIC_c < 2$.

Table 7. Scale and habitat variables influencing the probability of occurrence of primary cavity excavators according to the multi-model inference approach, in the black spruce forests of the Nord-du-Québec region, Quebec, Canada, 2003-2004.

Species	Habitat variables	Scale	Model-averaged estimate	Unconditional SE
Yellow-bellied Sapsucker	Large live trees (+)	Local	1.0×10^{-1}	3.8×10^{-2}
Hairy Woodpecker	---	---	---	---
American Three-toed Woodpecker	Woody debris (+)	Local	9.0×10^{-2}	4.2×10^{-2}
	Area of mature forests (+)	Local	2.0×10^{-4}	8.6×10^{-5}
Red-breasted Nuthach	Large live trees (+)	Local	1.2×10^{-1}	5.1×10^{-2}
Black-backed Woodpecker	Area of mature forests (+)	Landscape composition	2.9×10^{-6}	1.3×10^{-6}
Boreal Chickadee	Area of clearings (-)	Landscape composition	-2.0×10^{-7}	1.0×10^{-7}
Northern Flicker	Area of clearings (+)	Landscape composition	1.2×10^{-6}	5.0×10^{-7}
	Distance to unlogged mature forests (-)	Landscape configuration	-1.4×10^{-4}	7.0×10^{-5}

Table 8. Scale and habitat variables influencing the abundance of primary cavity excavators grouped in functional groups according to the multi-model inference approach, in the black spruce forests of northwestern Quebec, Canada, 2003-2004.

Functional groups	Habitat variables	Scale	Model-averaged estimate	Unconditional SE
All woodpeckers	Woody debris (+)	Local	3.6×10^{-2}	1.6×10^{-2}
	Length of edges (-)	Landscape configuration	-1.9×10^{-5}	9.3×10^{-6}
	Distance to unlogged mature forests (-)	Landscape configuration	-6.9×10^{-5}	2.6×10^{-5}
Large woodpeckers	---	---	---	---
Small woodpeckers	Woody debris (+)	Local	4.3×10^{-2}	1.8×10^{-2}
Weak cavity excavators	Area of mature forests (+)	Local	9.7×10^{-5}	3.8×10^{-5}

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ANTHROPOGENIC EDGES: THEIR INFLUENCE ON THE AMERICAN THREE-TOED WOODPECKER (*PICOIDES DORSALIS*) FORAGING BEHAVIOUR IN MANAGED BOREAL FORESTS OF QUEBEC

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Abstract: We studied edge effects on the American Three-toed Woodpecker (*Picoides dorsalis*) foraging behaviour in 18 remnant forest edges of the black spruce and feather moss forests managed with a checkerboard pattern of clear-cuts. Our objectives were to assess (1) the characteristics of foraging substrates used by woodpeckers, (2) whether birds foraged according to the availability of high-quality foraging substrates found at varying distances from edges and (3) to characterize the movement patterns of foraging individuals near clear-cut boundaries. Behavioural observations of individuals allowed us to characterize all trees used for foraging according to their DBH, decay state, bark cover, tree species and top condition. We also georeferenced those trees, which allowed us to determine their distance from the edge and the orientation of the bird movements with regards to the edge. We sampled snags and downed woody debris along 80 m line transects that were oriented perpendicularly to the edge. Our results show that woodpeckers foraged in a relatively high proportion of live trees (35%). For live trees, woodpeckers used trees of larger diameter and black spruce was underused with regards to its availability. Among snags, woodpeckers preferred snags with a larger diameter, a lower decay class and a higher bark cover than neighbour snags. The density of high-quality foraging substrates (large recently dead trees) increased near the edge and decreased as we got farther into the forest. When comparing the distribution of used foraging snags with the one of available high-quality foraging substrates, our results show that these two distributions are significantly different. High-quality substrates located at 40 m or less from an edge were used less frequently than their availability. Hence, we can conclude that foraging woodpeckers can use snags near edges but are less prone to use these foraging trees even though they become more available than elsewhere in remnant stands of managed forests. Nevertheless, bird movements were oriented parallel to the edge as far as 80 m from the clear-cut boundary. Considering the under-utilisation of high-quality substrates near edges, we suggest that food resource availability cannot explain the results obtained; the hypothesis that edges are acting as movement conduits likely explain woodpecker movement patterns we observed. Finally, the retention of larger tracks of mature and overmature forests would reduce the amount of edge habitat and provide better foraging conditions for American Three-toed Woodpecker in extensively managed landscapes.

Keywords: *edge effect, American Three-toed Woodpecker, dispersed clear-cuts, boundary*

Introduction

Fragmentation induced by forest harvesting generates sharp edges that are very dissimilar from natural boundaries found in unmanaged landscapes, in terms of vegetation composition and structure, length and distribution in the landscape (Matlack and Litvaitis 1999). Forest-dwelling birds can nonetheless use these sharp edges that can vary in depth with regards to habitat type, for different purposes. For instance, some of them use linear forest remnants, which are constituted of edge habitat given their narrow width (Mascarúa-López 2005; Mascarúa-López et al. 2006), as movement corridors to enhance dispersal of individuals and to avoid crossing open habitats (Machtans et al. 1996; Brooker et al. 1999; Sieving et al. 2000). Indeed, clear-cuts can effectively be perceived by birds as hostile areas even though they are vagile organisms. For instance, Machtans et al. (1996) showed that in the boreal mixed-wood forest region of Alberta, forest bird species movements were more frequent within corridors adjacent to clear-cuts as compared to cut blocks themselves. In a forested landscape fragmented by agriculture, Desrochers and Fortin (2000) also showed that chickadee flocks tended to move parallel to boundaries up to 100 m away within forest remnants. The presence of edges can therefore influence bird behaviour even at a relatively great distance.

On the other hand, some species might be more sensitive to edges and, thus, avoid such habitats (Kuitunen and Mäkinen 1993; Villard 1998; Huhta et al. 1999). The American Three-toed Woodpecker (*Picoides dorsalis*), considered a late-successional species (Virkkala 1987; Conseil canadien des ministres des forêts 1997; Imbeau et al. 1999; Imbeau et al. 2001) is thought to be one of these sensitive species. Fayt (1999) showed that in Finland, its close counterpart, the European Three-toed Woodpecker (*Picoides tridactylus*), foraged mainly on bark beetles found on spruce stems associated with forest interior conditions. According to this study, individuals may show a lower foraging effectiveness in fragmented mature forests as the proportion of forest interior habitat diminishes (Fayt 1999). Nonetheless, we still lack knowledge as to what minimal distance the interior forest conditions take place and what is the magnitude of this possible edge effect. The presence of clear-cut edges may then negatively affect foraging behaviour of some boreal woodpeckers. To the contrary, in North

American boreal forests, Imbeau and Desrochers (2002) failed to show that its North American counterpart, the American Three-toed Woodpecker, was negatively affected by human-induced edges within remnant forests of aggregated clear-cuts in Quebec, Canada. In this case, the greater availability of dead trees near clear-cut edges (Mascarúa-López 2005; Mascarúa-López et al. 2006) may compensate for the loss of mature and old-growth forests since American Three-toed woodpeckers are closely associated with standing dead wood (snags) for nesting and foraging (Leonard 2001). Edges induced by forest harvesting are effectively prone to show a high rate of windthrow caused by the increased velocity of wind after clearing (Franklin and Forman 1987; Esseen 1993; Darveau et al. 1995; Ruel et al. 2001). Furthermore, because of its life history traits, this species might be adapted to forest fragmentation that occurs within the range of variability of the natural disturbance regime. In the black spruce forests of Quebec, the level of fragmentation caused by the extensive areas of adjoining clear-cuts may nevertheless be outside this range of natural variation (Leduc et al. 2000; Bergeron et al. 2002)

Consequently, if we aim to manage the boreal forest while preserving its biodiversity, it is imperative to understand how forest-dwelling species respond to such changes in their environment. Hence, the main goal of our study was to document how the American Three-toed Woodpecker foraging behaviour is affected by the presence of human-induced edges. More specifically, our objectives were to assess (1) the characteristics of foraging substrates used by woodpeckers, (2) whether the distance from boundaries affects the distribution of foraging substrates used by woodpeckers and particularly high-quality foraging trees, (3) whether birds foraged according to the availability of high-quality foraging substrates found at varying distances from edges and (4) whether bird foraging movements were oriented parallel to edges and if so, whether the proximity of edges induced a higher rate of parallel movements compared with movements conducted at a greater distance from edges.

Study area

The study area was located within the black spruce and feather moss bioclimatic zone (Robitaille and Saucier 1998) of the north-western Quebec region (49°43' to 49°53'N and 75°44' to 76°26'W) and covers an area of 918 km². Since our study area is located on public lands, logging activities have substantially modified its landscape structure over the last two decades; the dispersed clear-cuts areas and the well-developed road networks have spread throughout these natural forest landscapes, leaving only relatively small blocks of remnant virgin forests that are 85-100 ha in size (MRNQ 2003). Cut blocks adjacent to our sampling sites were harvested from 1995 to 2002, and now constitute regenerating forests between 3 to 10 years old. Remnant patches are composed of mature and old growth forests (> 90 years old) in which black spruce (*Picea mariana*) is the dominant tree species with sparsely distributed jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), larch (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). The topography is flat with some scattered low elevation hills. The proglacial Ojibway lake has left glaciolacustrine deposits on the land while depressions are covered by clay deposits (Vincent and Hardy 1977). The mean temperature ranges from -2,5 to 0,0 °C and the mean annual precipitation ranges from 800 to 900 mm (Robitaille and Saucier 1998).

Methods

Behavioural observations of foraging American Three-toed Woodpecker

Behavioural observations were carried out in 2005 during the month of May. We broadcasted the drumming and calls of American Three-toed Woodpecker within the remnant forests at 40 m from the nearest clear-cut edge to attract individuals. We chose this distance to give the bird the option of moving deeper into the forest or closer to the edge to resume its foraging activities. When an individual responded, we followed him until he flew out of sight, blazing all trees used by foraging individuals. On foraged trees, we recorded the DBH (diameter at breast height), the deterioration state (Table 1) following Imbeau and Desrochers

(2002a), the top condition (intact/broken), the bark cover (1) 100% present, 2) ≥95% present, 3) between ≥75 and <95% present, 4) between ≥50 and <75% present, 5) between ≥25 and <50% present, 6) between ≥ 5 and <25% present, 7) between ≥1 and <5% present and 8) 0% present) and the tree species. We recorded the same variables for the nearest available stems and for the nearest available stems in the same state (live/dead) as the foraged stems. Neighbour trees were chosen according to their base-to-base distance from the foraged trees. Foraging trees were also georeferenced with a GPS Trimble GeoExplorer XM Pocket PC which had a precision of ± 1 m; this procedure allowed us to compute the distance from the clear-cut edge of trees used for foraging with the Arc GIS 9.0 computer program. We also computed the angle formed between each movement made by individuals and the edge, a movement representing the linear distance between two foraging trees (Figure 1).

Dead wood availability

We sampled snags and downed logs within 28 forest remnant edges of dispersed clear-cuts. The sampling was conducted along three transects per edge; transects were initiated at the clear-cut boundaries and extended 80 m deep into the forest patches to capture the entire edge effect gradient. The DBH, the deterioration state, the top condition, the bark cover and the tree species were recorded for all stems; these stems were then classified in four categories according to their distance from the clear-cut edge: 0-20 m, 20-40 m, 40-60 m and 60-80 m. We also noted the presence of foraging signs such as flaked bark and foraging holes (signs made mostly by the American Three-toed Woodpecker in our study area, and to a lesser extent by Black-backed Woodpecker) to quantify whether past foraging activities of woodpeckers were similar to those occurring currently in terms of the distance from the edge.

Variables that may influence windthrow within edges

To better understand the potential causes of windthrow near clear-cut edges, we measured a series of variables known to influence tree mortality: 1) edge exposure (Ruel et al. 2001), 2) edge exposure to the north-west (Mitchell et al. 2001), 3) time since logging and 4) edge orientation. For the edge exposure to the north-west, we chose this cardinal direction

since our study area is located in a region where dominant winds come from the north-west direction.

Statistical analyses

All the following analyses were done using the SPSS 10.0 program. First, we conducted case-control logistic regression models to determine whether foraging birds preferred live or dead trees and if, among dead trees, they showed a preference for standing over downed logs. We then conducted univariate case-control logistic regressions with the following tree characteristics taken separately to determine which ones were important for foraging birds: 1) DBH, 2) deterioration classes, 3) top condition, 4) bark cover and 5) tree species. The "cases" represented trees used by individuals, and the "controls", the nearest neighbour trees for the first two analyses and the nearest neighbour trees in the same state (live or dead) for the other analyses. The response variable was binary and defined as (1) utilization and (0) non-utilization of trees. However, since the response variable was set equal to one for all cases, we added a fictive case that took a value of zero to allow SPSS to perform correctly the logistic regression models. For this new case, the explanatory variables all had a value of zero. To make SPSS run properly the case-control option of logistic regression models, the explanatory variables were defined as the difference between the case and the control values for all cases. For instance, we computed the differences between the DBH of used (case) and neighbour snags (control) and this new variable was entered into the model. The variable "difference" can take negative or positive values or zero. The statistical analyses were based on the negative and positive values, so both must be represented at least once among all cases. When performing the analysis concerning the characteristics of live trees, the variable "difference, tree species" had only negative values and zeros so we added a dummy case which took a positive value for the latter variable and a value equal to one for the response variable. The same procedure was taken with the analysis on bird preferences for standing or fallen snags. In all analyses, each individual bird was considered a statistically independent unit to avoid pseudo-replication (Desrochers 1992), except in two cases : 1) in the analysis aiming to assess whether foraging birds preferred standing over

fallen snags, since the sample size would have been too small (n = 42 stems, 11 woodpeckers) and 2) in the analysis of live trees with the explanatory variable "difference, tree species". For these two analyses, we considered the sample size as being equal to the number of used stems instead of weighting cases according to the number of individual birds.

Our predictions were that 1) woodpeckers should forage more frequently on snags, 2) birds should choose the largest snags and the less deteriorated ones, and 3) among live trees, only large ones should be preferred. The previous analysis were necessary to identify high-quality foraging substrates in our study area.

We then used an analysis of variance with polynomial contrasts on the stem density (number of stems/ha) of all snags and downed logs to obtain a global portrait of dead wood distribution at varying distances from edges. The same analysis was also conducted to assess whether the distribution of high-quality foraging substrates, as defined by the previous case-control logistic regression models, was influenced by the distance from the edge. If the edge distance has an effect on the availability of such stems, the use of polynomial contrasts will determine more precisely the nature of this relationship. In some cases, the normality distribution and the variance homogeneity assumptions of the Anova were not met; consequently, we used the square-root, the fourth-root and the log transformations to meet these assumptions. We then calculated, for the 18 edges where behavioural observations were conducted, the proportion of recently dead large trees used by foraging woodpeckers by distance class (number of recently dead large trees used in a particular distance category / total number of recently dead large trees used in all distance categories). We performed a chi-square test to assess whether birds foraged on high-quality foraging substrates according to their availability with regards to distance from the edge. In this analysis, used foraging substrates were expected to follow the same distribution as the one obtained for available ones. The same test was done to compare distributions of high-quality foraging substrates with snags having foraging signs.

Our prediction concerning dead wood availability was that there should be more snags and downed woody debris near the edge and that the density should decrease as we

moved farther away into the forest. We expected that the spatial distribution of high-quality foraging substrates for American Three-toed woodpeckers would follow the same pattern. Woodpecker foraging response could show two contrasting patterns according to their edge sensibility: 1) birds showing no edge avoidance should forage on high-quality foraging substrates according to their availability or 2) birds showing edge avoidance should forage more often on trees located farther from the edge and overuse these trees according to their availability.

To assess whether the boundary affects the orientation of woodpecker movements between foraging trees and at what distance such an effect takes place, we followed the methodology developed by Desrochers and Fortin (2000) and we calculated the expected proportion of movements with an angle $\leq 20^{\circ}$ relative to the boundary (Figure 2). This threshold proportion of expected movements (22% within this $\leq 20^{\circ}$ range) represents our null hypothesis. If the observed proportion of movements parallel to the edge ($\leq 20^{\circ}$) is below this threshold, movements have no specific orientation, they are randomly oriented. To the contrary, if the observed proportion of movements $\leq 20^{\circ}$ relative to the edge is superior to this threshold, this implies that movements are oriented parallel to the edge. We also did a correlation analysis to determine whether the proportion of parallel movements was higher near the edge than farther away from it. Our prediction was that the proximity of the edge should increase the proportion of woodpecker movements with angle less or equal to 20° relative to the edge.

We finally conducted correlation analyses between the recently fallen snag density in the first 20 m of edges and the following variables: the year since logging, the edge exposure and the edge exposure to the north-west. A Kruskal-Wallis test was also done to compare the recently fallen snag density according to the edge orientation (N, S, E or W). We expected the fallen tree densities to be higher 1) as the edge exposure increased 2) as the edge exposure to the north-west increased, 3) as the adjacent clear-cuts got older and 4) within edges oriented towards the north.

Results

Characteristics of trees used for foraging

In our study sites, 65% of trees used by birds were dead (snags and logs) whereas live trees represented 35% of foraging substrates (Figure 3). However, when comparing used stems with the nearest unused ones, we notice that dead trees were overused with respect to their availability, but the difference was not significant (case-control logistic regression, n = 145 stems, weighted according to n = 25 woodpeckers, $\chi^2 = 1.865$, $p = 0.172$). Among dead trees used by foraging woodpeckers, 92.5% were snags whereas 7.5% were logs; when comparing used dead trees with the nearest available dead trees, snags were significantly overused with regards to their availability (case-control logistic regression, n = 42 stems, $\chi^2 = 5.062$, $p = 0.024$; Table 2; Figure 4). Individual case-control logistic regression models show that foraging woodpeckers used snags with a greater DBH (on average 17% larger), with a lower deterioration class and with a higher bark cover than neighbouring snags (Table 2; Figures 5, 6 and 7). For live trees, woodpeckers used trees of larger diameter (on average 15% larger) than neighbouring trees and black spruce trees were underused with respect to their availability (Table 3; Figures 5 and 8).

Edge effect on dead wood availability

The density of recently dead trees (class 4) was significantly higher near the clear-cut edge but there was no significant difference for intermediate (class 5), old (class 6) and very old (class 7) snags (Table 4). The density of stumps (class 8) also decreased as we moved away from the edge (Table 4). For downed woody debris, the effect of distance was significant for recently fallen snags (classes 9) and intermediate logs (class 10), which were more abundant near the edge than within the forest (Table 4).

When looking at stems DBH, the edge distance affected the distribution of snags larger or equal to 15 cm (Table 4), their density decreased as we moved away from the edge.

For large (DBH $\geq$ 15 cm) recently dead trees, there was a significant trend towards a higher density near the clear-cut edges of our study sites (Table 4).

Edge effect on trees used by foraging woodpeckers

Overall, 22% of the foraging trees were located within the forest interior habitat, c.a. farther than 80 m from edges, whereas 60 % and 18 % were within edges and in cut blocks, respectively. Large recently dead trees used by foraging birds are equally distributed within the edge, whereas available large recently dead trees are more abundant near the boundary. The chi-square test revealed that the distribution of used foraging substrates did not fit with the distribution of available foraging substrates with regards to distance from the edge ($\chi^2 = 11.833$, $p = 0.008$). Figure 9 indeed shows that, in the first 40 m away from the edge, foraging substrates are underused compared to their availability and they are overused in the 40-60 and 60-80 m distance categories. The distribution of snags with foraging signs was also significantly different from the distribution of large recently dead trees with regards to distance from the edge ($\chi^2 = 12.564$, $p = 0.006$; Figure 10).

Woodpecker movements along the edge

Across all distances, our observations were above the random movements' breakpoint of 22.2% indicating that birds moved often parallel to the edge (Figure 11). Moreover, as woodpeckers got closer to the edge, regardless of the side (cut block side or interior forest side), a higher proportion of their movements was parallel to the edge. This trend was not, however, significant at the 0.05 level (Spearman correlation, $\rho = -0.700$, $p = 0.094$; Figure 11). The 80-100 m distance category contained 26 observations that ranged from 80 to 185 m from the edge. We grouped them because their sample size was insufficient to generate distinct classes away from edges. Only nine trees were located in the 80-100 m distance category, while 17 were situated farther than 100 m from the edge.

Potential causes of windthrow within edges

None of the variables measured were significantly associated with the density of fallen trees within the first 20 m of forest away from the edge (Table 5).

Discussion

Characteristics of trees used by foraging woodpeckers

Our first prediction that birds should forage more frequently on snags than on live trees was partly supported. Overall, the American Tree-toed Woodpecker foraged twice as much on dead trees than on live trees. However, when looking more closely at the used vs. available trees and snags, the difference between dead and live foraging trees was not statistically significant with regards to the availability of the nearest neighbour tree. The proportion of live trees used by foraging woodpeckers was indeed relatively high (35%), indicating that during the spring season, this species may rely not only on snags but also on live trees to satisfy its energetic requirements.

Among live trees, we expected birds to forage more on large stems; our results effectively showed that larger live trees were preferred over smaller ones. On the other hand, black spruce did not seem to be the preferred tree species. In fact, woodpeckers foraged less on black spruce than what was predicted by its availability. Many of the foraged live trees were balsam firs located within the forest patches or within cut blocks, on which woodpeckers sap licked. Among the 24 individuals followed, 13% used the sap licking technique. This foraging behaviour has been documented in some parts of Europe (Glutz von Blotzheim and Bauer 1980) but in North America, this behaviour has seldom been reported (Short 1974, 1982; Villard 1994 but see Imbeau and Desrochers 2002a). We however noticed that American Three-toed woodpeckers sap licked from the spring time until early June and that birds stopped afterwards. At that time of the year, the sap of trees is the most abundant and nutritious (D. Gagnon, pers. comm.) and birds may take advantage of this

temporary food supply. Our second prediction that foraging birds should choose the largest and the less deteriorated snags was supported by our results. Imbeau and Desrochers (2002a) obtained similar results; in their study, the mean DBH of snags used by foraging woodpeckers was 19.2 cm. Goggans et al. (1989) also showed that American Three-toed woodpeckers foraged mainly on trees with a DBH greater than 17.5 cm. In the study of Imbeau and Desrochers (2002a), recently dead trees were also preferred over older snags, which is consistent with our results. Analyses showed that among dead trees, birds foraged most often on standing snags compared with downed logs, these results being consistent with those of Murphy and Lehnhaussen (1998) and Imbeau and Desrochers (2002a).

Edge effect on dead wood availability

Several studies have documented tree mortality within human-induced edges (Franklin and Forman 1987; Esseen 1993; Darveau et al. 1995; Mascarúa-López 2005). In the study of Mascarúa-López (2005), it is shown that the log density is higher in the first 10 m from the clear-cut edge but, conversely, there is no edge effect on snags, whatever their deterioration state. Our results show the same patterns whereas recently fallen snag density is higher near the edge and decreases linearly as we move away from it. However, we were able to detect a positive edge effect on stumps (< 2 m high) and on recently dead trees, in both cases the densities being higher near the edge and decreasing linearly with distance from the edge. Following harvesting, increases in wind speed can induce a higher rate of broken stems and blowdown at clear-cut edges (Esseen 1993). In his study, Esseen (1993) indeed showed that following a clear-cut, the most common type of wind-induced mortality was uprooting (67%), stem breakage (24%) and trees that died standing (9%). In our study, recently fallen snags probably fell down after the opening of the adjacent area. Their bark was still present and basically intact, and the logs were not yet covered by mosses; in this area of the boreal forest, downed logs are indeed rapidly buried beneath a thick layer of mosses once they have reached the ground (Imbeau and Desrochers 2002a). Contrary to Mitchell et al. (2001) and to Ruel et al. (2001), we were unable to link the recently fallen tree density within the first 20 m of the edge to any characteristics of the adjacent clear-cuts. Neither the edge orientation nor the year since logging seemed to influence the fallen tree

density. On the other hand, older woody debris probably fell down before clearings and they were evenly distributed within forest edges. Recently dead trees were recruited, however, after harvesting. It is well documented that the microclimate at edges is quite different from conditions found within forest interiors; the solar radiation being more intense, the daily temperatures higher and the degree of humidity lower (McCollin 1998; Matlack and Litvaitis 1999). Elevated soil temperatures and changes in plant water use efficiency are in fact well established consequences of the increased exposure near the edge (Chen et al. 1993; Kapos et al. 1993). On the other hand, downed logs, while falling, can also have injured nearby trees, hence allowing fungi to penetrate them and bring about death. Esseen (1993) also found a positive relationship between the mortality of trees and their diameter, tree mortality being higher for large stems. Our results are consistent with this study since larger recently dead trees seem to be slightly more abundant near edges than all recently dead trees pooled together.

Do foraging woodpeckers avoid edge habitat?

Our prediction concerning edge avoidance by the American Three-toed Woodpecker was partly supported by the data. Foraging trees were evenly distributed from the edge to the forest interior whereas high-quality foraging substrates, c.a. large recently dead trees, were, however, more abundant near the boundary. Hence, even though birds did not avoid feeding near edges, they did not forage on those trees in proportion to their availability. Moreover, our results not only reflect the current response of birds to edges, but the same response is obtained for past foraging signs indicating some level of consistency in the foraging patterns of this species over time since timber harvesting. Our results thus indicate that foraging American Three-toed woodpeckers can use snags near edges but are less prone to use these foraging trees even though they become more available than elsewhere in remnant stands of managed forests. Our results thus corroborate the findings of Imbeau and Desrochers (2002b), that concluded there was no edge-avoidance pattern from foraging American Three-toed Woodpecker in shredded forests of aggregated clear-cuts.

The higher proportion of foraging movements oriented parallel to the clear-cut edge near the edge indicates that individuals move less freely in all directions near edges than within interior forest conditions. This suggests that when American Three-toed woodpeckers forage near and at edges, they avoid moving far into harvested timber open habitats, which are likely to be more risky environments with regards to predation risk. On the other hand, woodpecker parallel movements relative to the edge also occurred at a greater distance from the edge, where available foraging substrates were less abundant. Hence, this result suggests that the "movement conduit" hypothesis, rather than the food resource availability hypothesis, explains the observed pattern of movements along edges. In their study Desrochers and Fortin (2000) showed that chickadee flocks tended to move parallel to boundaries more frequently when moving near edges; our results follow the same pattern even though our relationship is not significant (although $p < 0.1$). This can partly be explained by the fact that woodpeckers can use foraging substrates within clear-cuts, when such substrates are available and suitable. They are indeed not as constrained within the edge as it is the case for chickadees, for which there were no foraging substrates available within agricultural fields. In the Desrochers and Fortin's (2000) study, edges also influenced the orientation of movements as far as 125 m within the forest. Our results point in the same direction since woodpecker movements were oriented parallel to the edge at least until 80 m from the boundary.

Contrary to Fayt (1999), we did not sample bark beetle availability, so we can not link prey distribution with woodpecker substrate selection with regards to edge location. Nevertheless, given that large recently dead trees were more abundant near edges, we could hypothesize that woodpeckers foraging would be more efficient because large stems generally support higher larvae densities (Nappi et al. 2003). Alternately, Fayt (1999) found that woodpecker preys are less uniformly distributed and less abundant on snags exposed to open habitat compared with those located in the forest interior. Moreover, Fayt (2004) also showed that the bark beetle species richness responded to edge vicinity in remnant forest patches surrounded by harvested surroundings, increasing towards the inner part of the forest. This could partly explain why foraging woodpeckers did not preferentially use edge habitats in our study, even when foraging substrates were more abundant; this higher availability of

substrates being offset by a presumed lower abundance of insect preys and a lower species richness in these substrates. According to Fayt (2004), the bark beetle species richness would be positively related to the abundance of wood-boring beetles (longhorn beetles), whose larvae are an important part of adults and offspring diet during the summer months and/or the reproduction (Hogstad 1970). On the other hand, it has been shown that European three-toed woodpeckers diet was mainly composed of bark beetles (*Scolytidae*) from autumn to spring time (Fayt 1999), hence emphasising the switch in preferential preys in the woodpeckers diet with respect to the period of the year. Consequently, forest/clear-cut edges in our study may have supported a lower number of preferred prey species for this period of the year, leading to an underuse of what appears to be high-quality foraging substrates.

Haila (1983) showed that American Three-toed Woodpecker can have a relatively large territory. In its experiment, the smallest island colonized by woodpeckers was 99 ha (Haila 1983), but in highly fragmented habitats, we can expect their territory to reach three-fold this size (Mykrä et al. 2000). One single territory can then encompass numerous artificial edges in a managed landscape of dispersed clear-cuts since remnant blocks must have 85-100 ha in size (MRNQ 2003). Thus, individuals may perceive the landscape in a fine-grained manner. Costs in terms of time, energy and exposure to predators can then be incurred when individual movements occur between several habitat patches (Hinsley 2000). However, before extensive forestry spread over pristine boreal forests, habitat fragmentation was naturally generated by wildfires and windthrows (Bergeron 1991; Johnson 1992; Payette 1992; Angelstam 1997; Gauthier et al. 2001; Bergeron et al. 2004). The American Three-toed Woodpecker evolved under these natural conditions and may be well adapted to cross large open habitats when searching for food resources. Hence, this species may be quite resilient to habitat loss and fragmentation generated by forest harvesting. However, burned areas represent a less hostile environment since, generally speaking, islets of live trees, partially burned and dead trees are spread throughout those areas (Leduc et al. 2000; Haeussler and Kneeshaw 2003), providing suitable foraging substrates for American Three-toed woodpeckers and other species.

Management implications

Since foraging American three-toed woodpeckers are less prone to forage near clear-cut edges, the extent of boundaries at the landscape level may have an impact on this species' behaviour. In fact, landscapes showing a large amount of edge habitat combined with a low proportion of forest interior conditions, such as linear forest remnants of aggregated clear-cuts, may become less suitable habitats for foraging individuals. Those linear strips indeed support a lower abundance of American Three-toed Woodpecker (and of several other primary cavity excavator birds) than larger forest remnants of a dispersed clear-cuts pattern (Gagné, chap. 1). The dispersed clear-cutting pattern nevertheless generates a large amount of edges, particularly when the proportion of remaining habitat turns around 50 % (Franklin and Forman 1987). Hence, the retention of larger tracks of mature and overmature forest would reduce the length of edges and, conversely, enhance the amount of forest interior habitat. This in turn could provide better foraging conditions for American three-toed woodpeckers and, perhaps, other forest-dwelling species.

List of figures

Figure 11. Observed proportion of movements parallel relative to the boundary (black dots) and expected percentage of movements with angle less than or equal to 20° relative to the edge (dashed line), Nord-du-Québec, Quebec, Canada, 2004-2005. The tendency curve (black line) was added *a posteriori*.

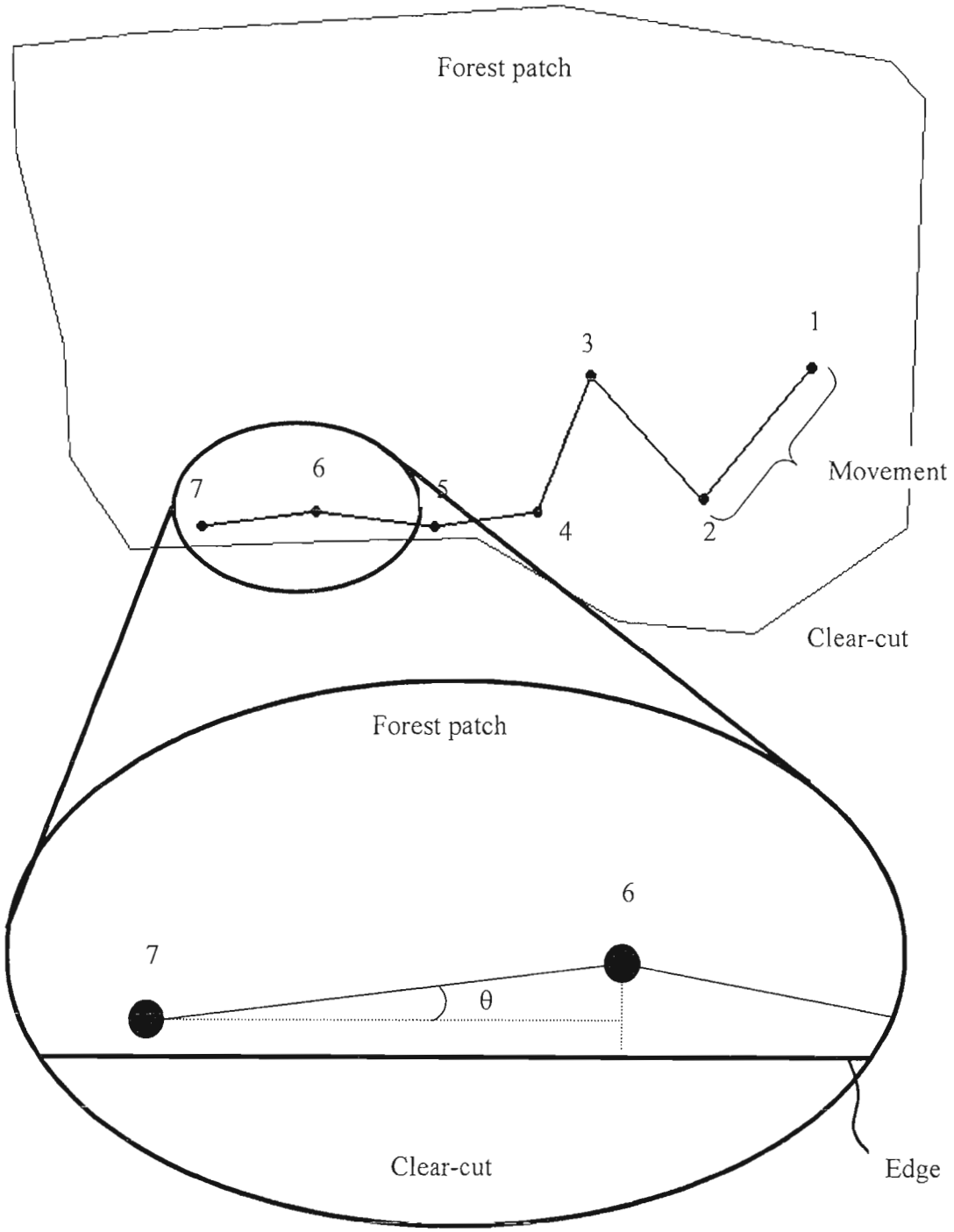
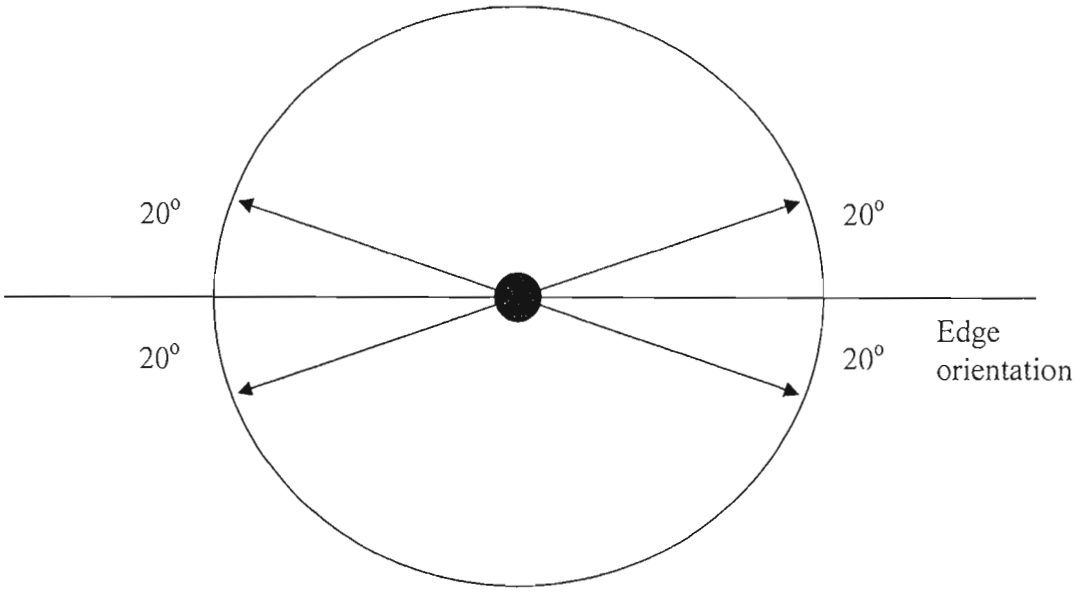


Figure 1. Gagné et al.



The black dot represents an individual who has the option to move in all directions relative to the forest /clear-cut boundary. By considering all movements with angles $\leq 20^{\circ}$ relative to the edge as parallel to the edge, the null hypothesis of random movements equals to $80^{\circ} / 360^{\circ} \times 100 = 22.2\%$. Below this value, movements are considered as random (unaffected by edge presence).

Figure 2. Gagné et al.

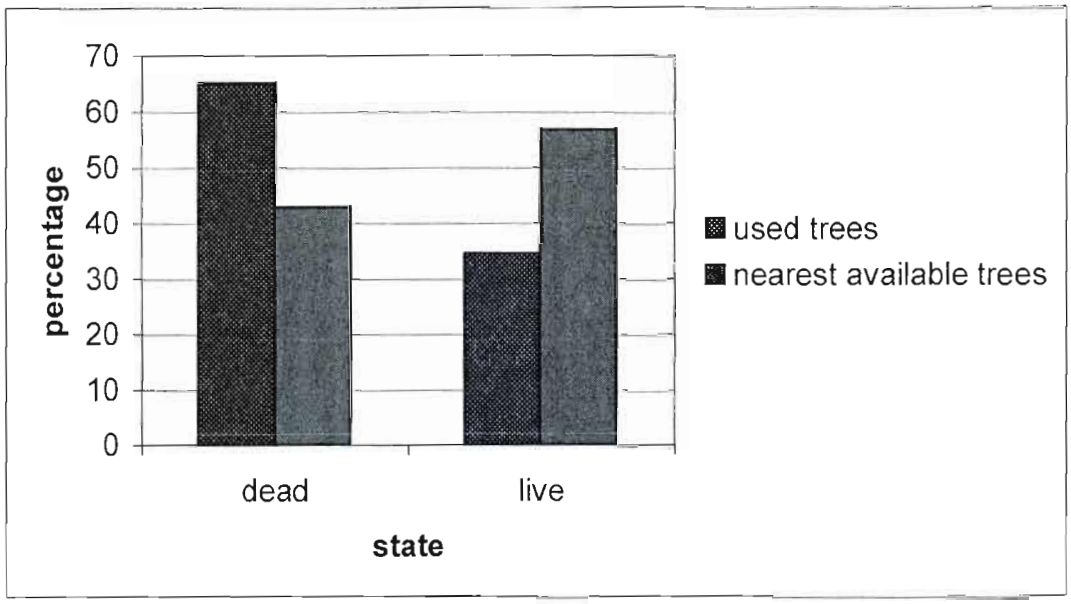


Figure 3. Gagné et al.

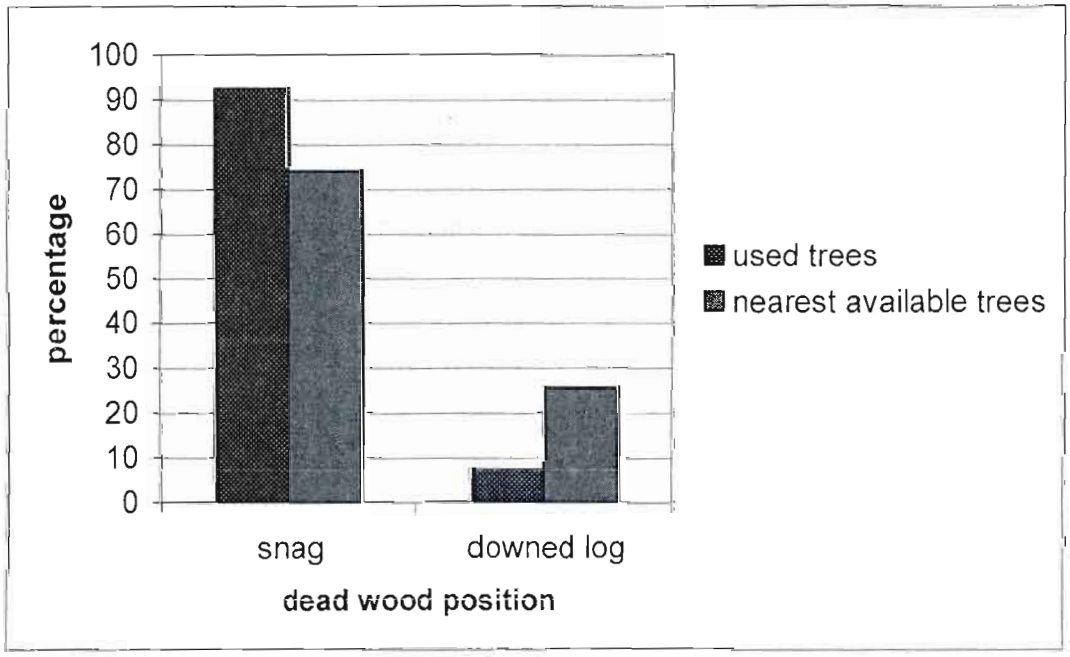


Figure 4. Gagné et al

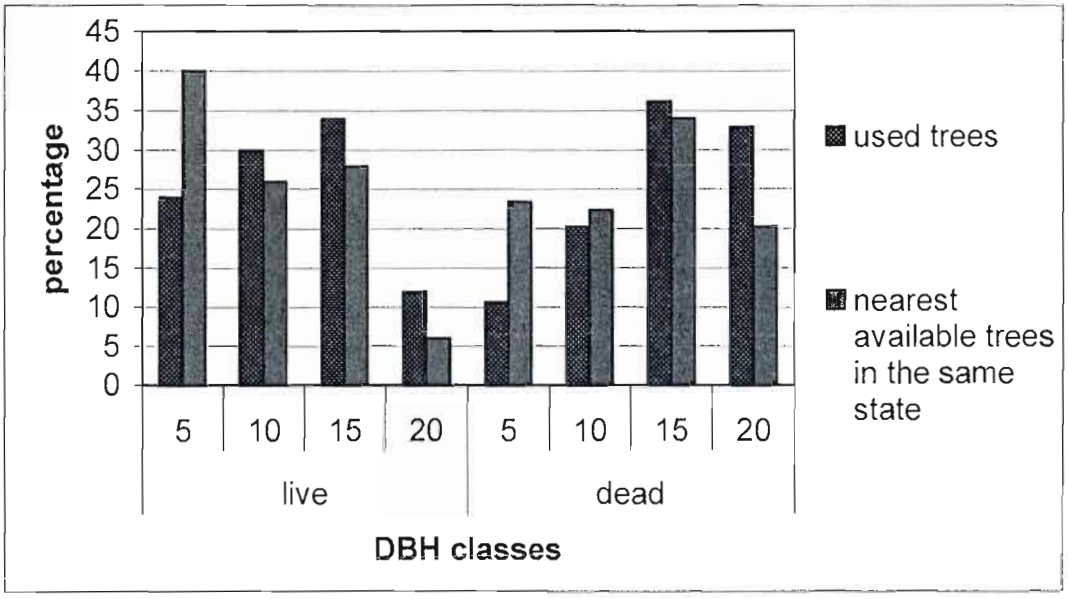


Figure 5. Gagné et al.

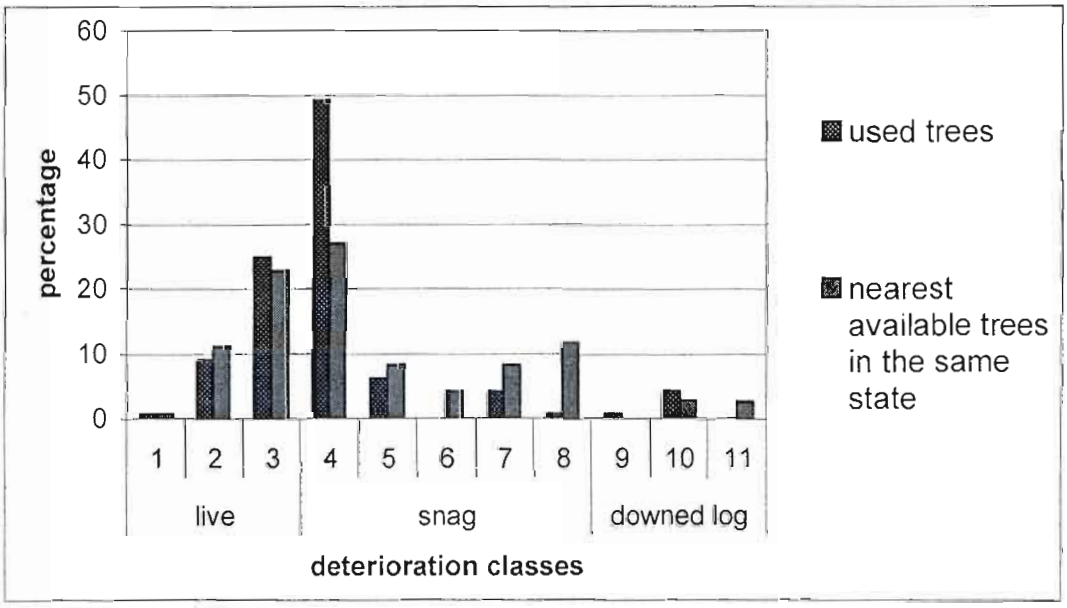


Figure 6. Gagné et al.

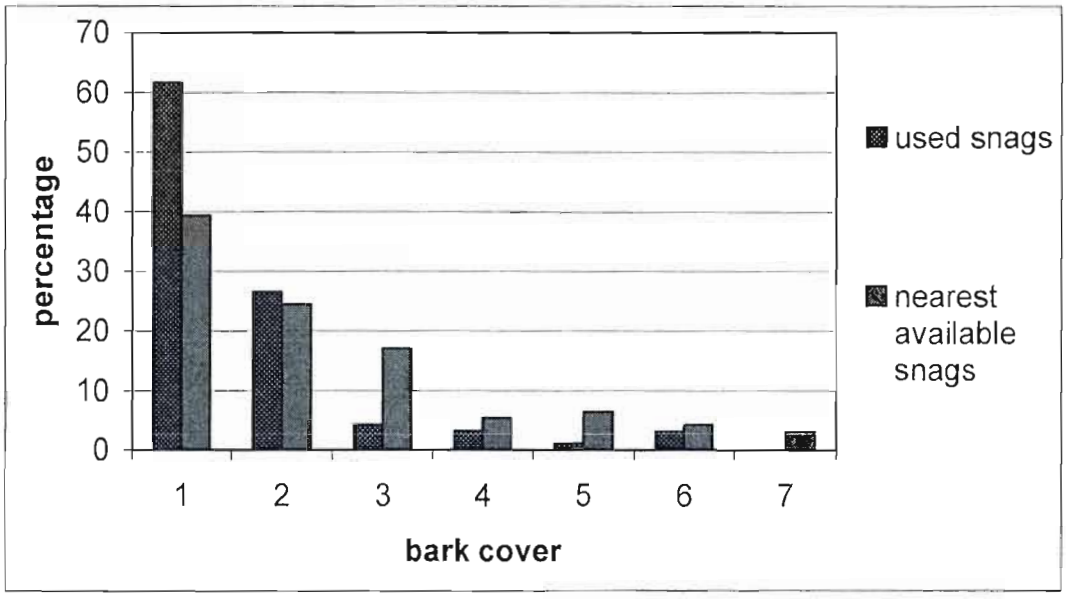


Figure 7. Gagné et al.

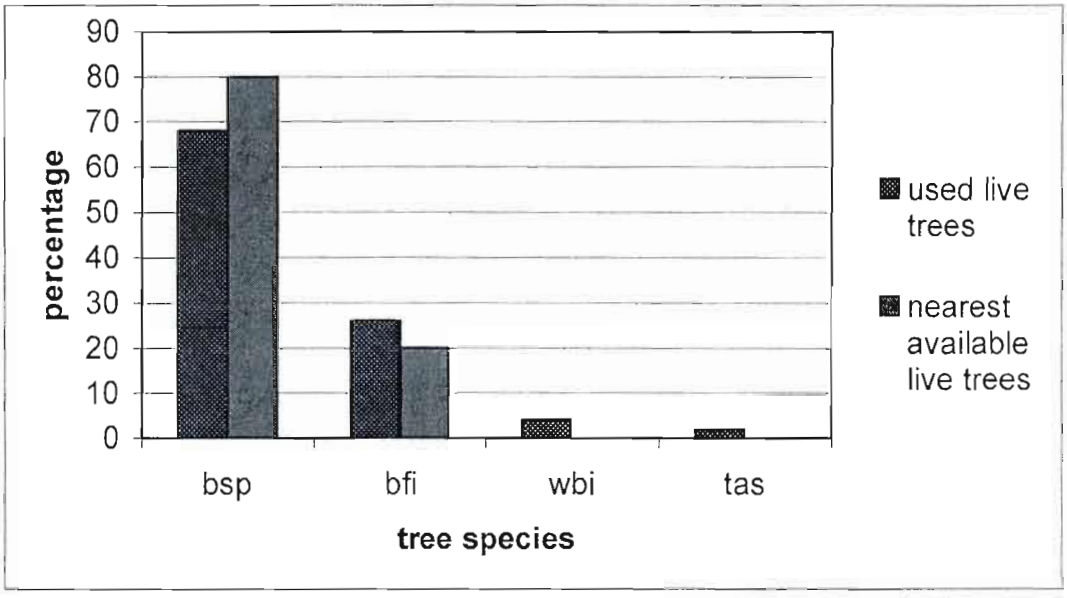


Figure 8. Gagné et al.

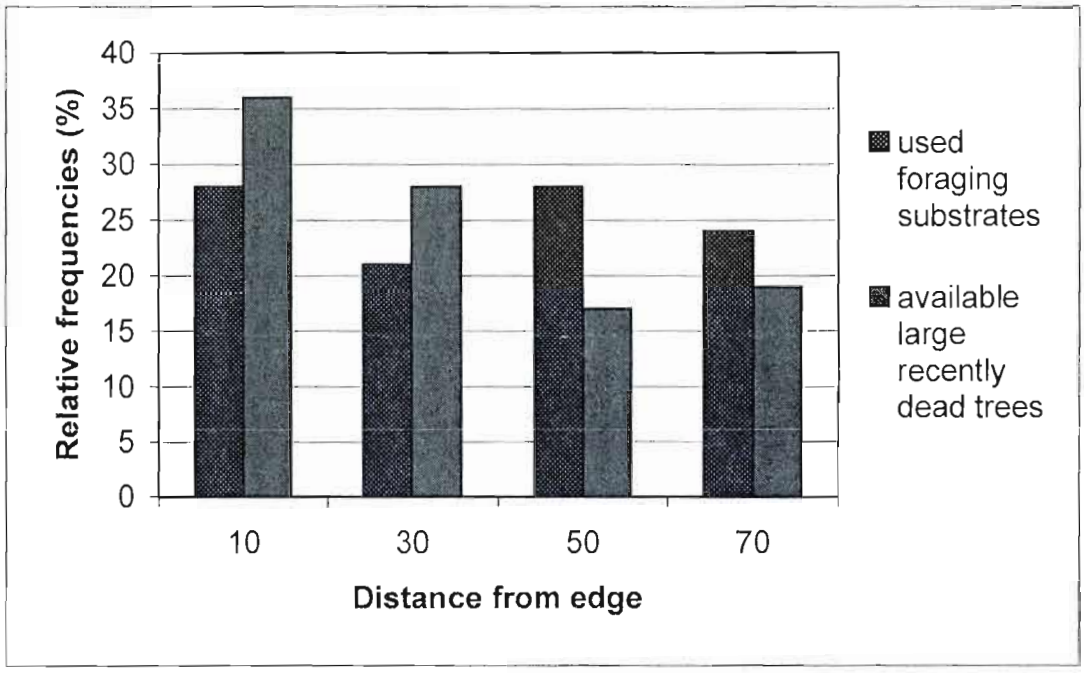


Figure 9. Gagné et al.

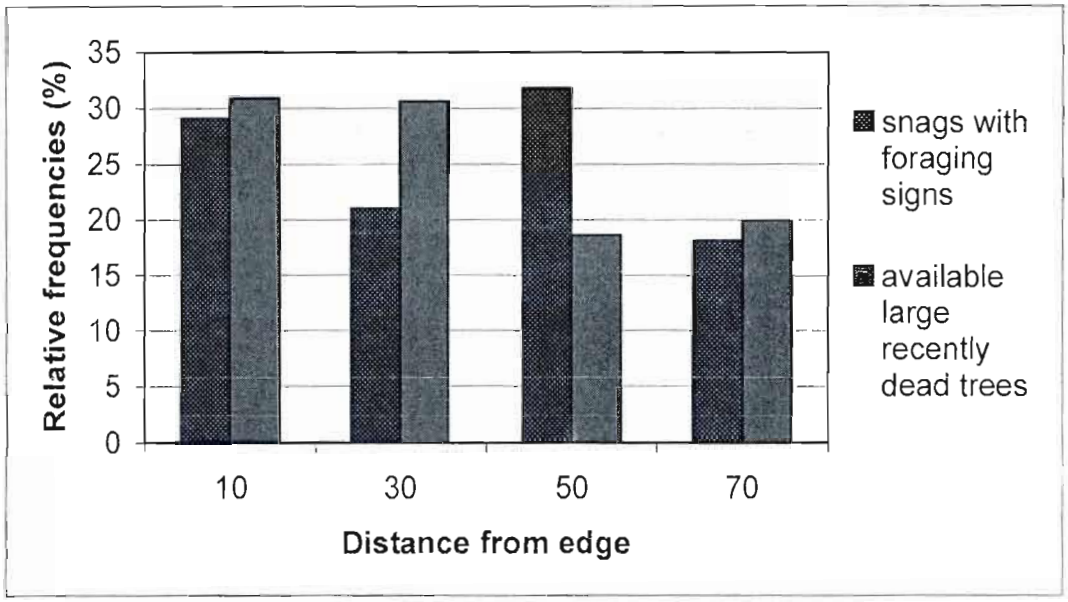


Figure 10. Gagné et al.

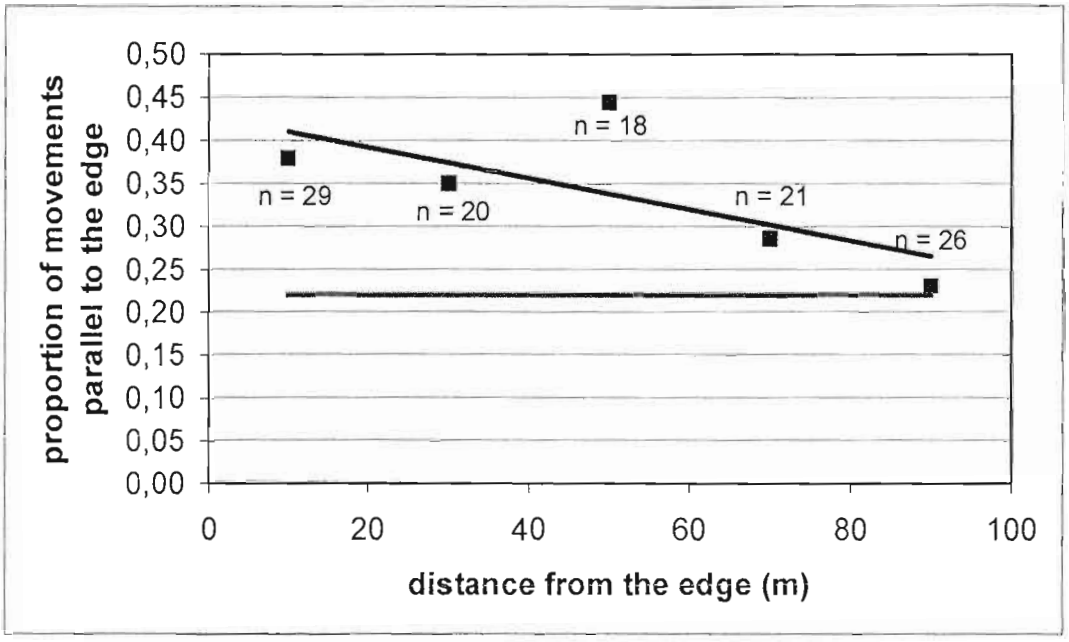


Figure 11. Gagné et al.

Table 1. Characteristics of live trees, snags and downed logs according to their deterioration state, Nord-du-Québec, Quebec, Canada, 2004-2005.

Deterioration class	Tree characteristics
Live trees	
1	Alive and healthy, ≥95% foliage, no signs of deterioration
2	Declining, remaining foliage between ≥20% and <95%, senescent tree
3	Dying, <20% foliage remaining
Snags	
4	Recently dead, hard wood, firm bark cover, dead foliage and small twigs still remaining
5	Hard wood, firm bark cover, no dead foliage, no small twigs
6	Hard wood, loose bark cover, broken top, height still more than 50% of what is observed on trees with same DBH
7	Soft, decomposed wood, broken top with height less than 50% of what is observed on trees with same DBH
8	Stump, height <2 m
Downed logs[a]	
4	Recently fallen, hard wood, firm bark cover and small twigs still remaining
5	Hard wood, no dead foliage, no small twigs, bark cover still remaining but more easily removable
6	Wood still hard but less than the previous classes, loose bark cover, can be partially covered by mosses

[a] Downed logs were classified using the same numbers as for snags, but for analysis, all those dead trees were considered whether as (1) standing stems or (2) downed stems.

Table 2. Characteristics of snags used for foraging by American Three-toed Woodpeckers and nearest available snags, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Quebec, Canada, 2004-2005.

Characteristics	Used snags		Nearest available snags		Logistic regression	
	mean (median)	SE (range)	mean (median)	SE (range)	χ^2	p[c]
Diameter at breast height[a]	17.79	0.57	14.78	0.64	7.27	**0.007**
Deterioration class[a]	(4.00)	(4.00-8.00)	(5.00)	(4.00-8.00)	8.81	**0.003**
Top condition (% broken)[a]	22.99	4.54	19.54	4.28	0.66	0.416
Bark cover[a]	(1.00)	(1.00-6.00)	(2.00)	(1.00-7.00)	4.11	**0.043**
Tree species (%)[a]					0.02	0.886
Black spruce	88.51	3.44	86.21	3.72	-	-
Jack pine	6.90	2.73	5.75	2.51	-	-
Tremblin gaspen	2.30	1.62	1.15	1.15	-	-
White birch	2.30	1.62	3.45	1.97	-	-
Others	0.00	0.00	3.45	1.97	-	-
Snag position (% fallen)[b]	7.45	2.72	12.77	3.46	5.06	**0.024**

[a] Results are based on n = 24 woodpeckers, for a total of 87 pairs of snags.

[b] Results are based on n = 11 woodpeckers, for a total of 42 pairs of dead trees (snags and logs).

[c] Results in bold are significant at the 0.05 level.

Table 3. Characteristics of live trees used for foraging by American Three-toed woodpeckers and nearest available live trees, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Quebec, Canada, 2004-2005.

Characteristics	Used live trees		Nearest available live trees		Logistic regression	
	mean (median)	SE (range)	mean (median)	SE (range)	χ^2	p[c]
Diameter at breast height[a]	13.62	0.67	11.55	0.74	3.93	**0.048**
Deterioration class[a]	(3.00)	(1-3)	(3.00)	(1-3)	0.05	0.832
Top condition (% broken)[a]	4.00	2.80	2.00	2.00	0.35	0.555
Bark cover[a]	(1.00)	(1.00-3.00)	(1.00)	(1.00-3.00)	0.65	0.422
Tree species (%)[b]					3.96	**0.047**
Black spruce	68.00	6.66	80.00	5.71	-	-
Trembling aspen	2.00	2.00	0.00	0.00	-	-
White birch	4.00	2.80	0.00	0.00	-	-
Balsam fir	26.00	6.27	20.00	5.71	-	-

[a] Results are based on n = 51 pairs of live trees; data are weighted for n = 20 woodpeckers.
[b] Results are based on n = 51 pairs of live trees plus one fictive case; data are not weighted.
[c] Results in bold are significant at the 0.05 level.

Table 4. Mean density of snags and downed logs according to their deterioration and DBH classes and the distance to forest boundaries, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Quebec, Canada, 2004-2005. Means are followed by their standard errors. Results are based on n = 28 edges.

	Distance from boundary (m)								Anova	
	0-20		20-40		40-60		60-80		linear contrast	p [c]
Deterioration class										
snags										
4	130.4	(16.2)	97.0	(9.7)	85.0	(10.7)	97.6	(15.1)	-0.22[b]	**0.039**
5	98.2	(13.8)	116.1	(17.0)	87.0	(13.1)	87.0	(9.8)	-0.55[a]	0.448
6	56.6	(11.0)	47.1	(8.5)	40.5	(7.0)	58.9	(11.5)	0.04[a]	0.955
7	72.6	(10.4)	69.6	(9.4)	74.9	(10.4)	56.6	(7.7)	-0.45[a]	0.463
8	122.6	(15.0)	129.1	(16.5)	112.6	(12.5)	84.0	(10.6)	-1.46[a]	**0.026**
Downed logs										
4	28.0	(6.3)	17.4	(5.0)	9.6	(2.6)	9.6	(2.6)	-0.87	**0.007**
5	80.4	(12.2)	53.1	(10.5)	48.8	(8.9)	54.8	(8.5)	-1.43[a]	**0.030**
6	61.2	(7.4)	59.5	(10.6)	48.2	(8.2)	50.7	(6.0)	-9.59	0.248
DBH class										
5-9.5 cm	146.5	(18.8)	183.9	(26.8)	169.6	(22.9)	151.8	(17.0)	0.38	0.986
10-14.5 cm	161.9	(19.6)	129.8	(12.9)	118.4	(13.0)	131.6	(16.2)	-22.86	0.147
15-19.5 cm	109.6	(14.8)	92.8	(11.9)	77.9	(9.4)	66.1	(9.2)	-1.83[a]	**0.004**
≥20 cm	62.5	(12.9)	52.4	(10.8)	33.9	(7.0)	34.6	(6.2)	-1.61[a]	**0.032**
Foraging trees										
class 4, DBH ≥15 cm	52.9	(9.2)	41.1	(5.4)	30.4	(5.8)	29.2	(4.9)	-1.54[a]	**0.009**

[a] Anova has been conducted with the square root of the density.

[b] Anova has been conducted with the fourth root of the density.

[c] Results in bold are significant at the 0.05 level.

Table 5. Variables presumed to influenced the windthrow rate within the first 20 m of forest boundaries.

Variable	Description	Analysis	p
Time since logging	Years since logging of adjacent opening	Correlation	0.422
Edge exposure	Sum of distance across opening from segment for all eight cardinal directions	Correlation	0.836
Edge exposure north-west	Sum of distance across opening from segment for 0°, 270° and 315° only	Correlation	0.58
Edge orientation	Cardinal direction (N, S, E or W) of edges	Kruskal-Wallis	0.579

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CONCLUSION GÉNÉRALE

2.1 Occurrence des espèces excavatrices en coupes en mosaïque vs agglomérées

Le Pic à dos rayé et la Mésange à tête brune sont deux espèces dont la probabilité d'occurrence s'est avérée plus élevée dans les peuplements résiduels des coupes en mosaïque comparativement aux coupes agglomérées. Le Pic Flamboyant et le Pic Chevelu ont, quant à eux, montré une plus forte occurrence dans les habitats linéaires résiduels des coupes agglomérées. Ces résultats corroborent ceux obtenus lors d'études antérieures, ces études associant les deux premières espèces aux forêts matures et la troisième, aux milieux ouverts (Ehrlich et al. 1988 ; Conseil canadien des ministres des forêts 1997; Imbeau et al. 1999; Imbeau et al. 2001; Bevis et Martin 2002).

À court terme, les habitats linéaires des coupes agglomérées semblent représenter un habitat de meilleure qualité pour les excavateurs de grande taille (Pic Flamboyant) alors que les peuplements résiduels des coupes en mosaïque semblent être un meilleur habitat pour les excavateurs de petite taille ainsi que pour les excavateurs faibles. Les assemblages d'oiseaux se sont par conséquent avérés quelque peu différents entre les deux types d'habitats résiduels. Ces différences dans les assemblages d'espèces cavicoles excavatrices pourraient se répercuter sur la guilde des utilisateurs secondaires de cavités, pour qui la présence de cavités représente un facteur limitant leur établissement dans un peuplement forestier (Martin et Eadie 1999).

2.2 Composition et configuration du paysage

En forêt boréale, il a été montré que bien que la configuration des peuplements résiduels puisse affecter les espèces animales associées aux forêts matures et surannées, la composition des paysages influençait de façon plus importante le patron de distribution de ces espèces (Rosenberg et Raphael 1986; Hejl 1992; Drapeau et al. 2000). Nos résultats suggèrent par contre que les espèces à l'étude sont affectées non seulement par la perte de

forêts matures mais également par la configuration des peuplements forestiers résiduels à l'échelle du paysage. La présence des lisières semble en ce sens influencer l'occurrence de plusieurs espèces, tel que le montrent nos modèles de régressions logistiques hiérarchiques. Les effets de la configuration des paysages sont davantage susceptibles de se manifester à l'intérieur de notre aire d'étude, où les patrons de coupes en mosaïque et agglomérées génèrent une quantité faramineuse de lisières et repoussent toujours plus loin les massifs forestiers non fragmentés, que dans l'étude de Drapeau et al. (2000). En effet, dans cette étude, les massifs forestiers semblent se trouver en plus grande concentration à l'échelle du paysage, réduisant du même coup l'influence des variables de configuration sur les populations aviaires. De plus, l'échantillonnage mené dans l'étude de Drapeau et al. (2000) a été réalisé non pas dans les habitats linéaires résiduels mais à l'intérieur des massifs forestiers, ce qui pourrait réduire d'autant plus l'effet potentiel des variables de configuration du paysage. D'autre part, les effets négatifs que génèrent la perte d'habitat et la configuration du paysage en zone de coupes agglomérées semblent par contre avoir été atténués par l'abondance des attributs structuraux, tels que les chicots, dans les habitats linéaires résiduels, ces derniers étant utilisés lors de la nidification ainsi que pour l'alimentation de certaines espèces d'oiseaux excavateurs. La présence de ces espèces dans les habitats linéaires des coupes agglomérées, qui semblent représenter des habitats sub-optimaux, serait donc en partie liée à la forte abondance d'arbres morts arborant les divers stades de détérioration et les diverses classes de diamètre que l'on retrouve dans les peuplements résiduels des coupes en mosaïque.

2.3 Effets de lisière sur le comportement alimentaire du Pic à dos rayé

La présence de lisières abruptes induites par la coupe forestière engendre un évitement de ces dernières par le Pic à dos rayé lors de sa quête alimentaire et ce, malgré une plus forte abondance des bons substrats d'alimentation à proximité des bordures. Les bons substrats d'alimentation ont été caractérisés comme des arbres récemment morts de diamètre égal ou supérieur à 15 cm et dont l'écorce était pratiquement intacte, ces résultats corroborant ceux de Imbeau et Desrochers (2002a). Par contre, malgré le fait que les plus gros arbres

supportent généralement une plus forte densité de larves d'insectes (Nappi et al. 2003), cet avantage est susceptible d'être contrebalancé (1) par le fait que les larves de scolytes pourraient être moins abondantes et distribuées moins uniformément sur les arbres exposés aux milieux ouverts par la coupe, comparativement à ceux situés à l'intérieur de la forêt (Fayt 1999) et (2) par une plus faible richesse spécifique de scolytes à proximité des bordures de coupes forestières (Fayt 2004), la richesse en scolytes étant, selon (Fayt 2004), positivement associée à l'abondance des longicornes. En ce sens, les larves de longicornes contribuent de façon importante à l'alimentation des adultes et des jeunes en été et pendant la période de reproduction (Hogstad 1970). Ainsi, l'absence de certaines espèces de proies préférentielles du Pic à dos rayé en période printanière est susceptible d'avoir engendré une sous-utilisation des bons substrats d'alimentation à proximité des bordures de coupes forestières.

Par ailleurs, les individus qui s'alimentent à proximité des lisières tendent à se déplacer de façon parallèle à la bordure et ces mouvements non aléatoires s'étendent jusqu'à au moins 80 m à l'intérieur de la forêt résiduelle. À l'instar des travaux de Desrochers et Fortin (2000), un effet de canalisation des mouvements induit par la présence des bordures pourrait expliquer les mouvements non aléatoires observés à proximité ainsi qu'à une certaine distance des lisières.

2.4 Conséquences pour l'aménagement forestier

La composition et la configuration des paysages forestiers, telles que documentées dans cette étude, influencent la présence et l'abondance des espèces d'oiseaux excavateurs au sein des peuplements résiduels. La composition et la configuration des habitats résiduels sont donc des éléments importants à considérer pour les espèces associées aux forêts matures car ceux-ci pourraient jouer un rôle majeur dans la dispersion des individus ainsi que dans l'utilisation des peuplements résiduels comme habitat de reproduction. À ce titre, les habitats linéaires tels que les bandes riveraines ou les séparateurs de coupes en zone de coupes agglomérées pourraient s'avérer être des habitats sub-optimaux pour les oiseaux excavateurs (Gagné, chap. 1), car n'étant souvent que des habitats de bordure (Mascarúa-López 2005;

Mascarúa-López et al. 2006), ils ne comportent pas suffisamment de superficie dont les conditions structurales s'apparentent aux forêts âgées.

D'autre part, à long terme, les aires de coupes en mosaïque seront similaires, en termes de composition et de configuration des paysages, aux aires de coupes agglomérées puisque les blocs de forêts résiduelles seront coupés dès que la régénération adjacente aura atteint une hauteur de trois mètres (MRNQ 2003). Par conséquent, il serait temps d'innover dans le domaine de l'aménagement forestier si nous voulons contribuer au maintien de la diversité biologique en zones aménagées. En ce sens, l'implantation d'une approche écosystémique devrait être considérée par les gestionnaires et les aménagistes, cette dernière ayant fait l'objet de nombreuses études depuis plusieurs années (Galindo-Leal et Bunnell 1995; Leduc et al. 2000; Bergeron et al. 2001, 2004; Gauthier et al. 2001; Harper et al. 2002). Par ailleurs, à défaut d'implanter une telle approche, il serait impératif de maintenir des massifs de forêts mûres et surannées non perturbés par la coupe au sein même des aires de récolte afin de conserver un habitat de qualité, constitué de forêt intérieure, pour l'alimentation et la nidification des oiseaux excavateurs et d'autres espèces animales. Le maintien des chicots et des arbres verts, seuls ou en îlots, pourrait également augmenter l'utilisation des parterres de coupes par les oiseaux excavateurs. En ce sens, Nappi (2000) a noté que le Pic à dos rayé fréquentait les îlots résiduels ainsi que les bordures de brûlis. La rétention d'éléments de structure dans les parterres de coupe contribuerait donc à rendre ces milieux moins hostiles, ainsi qu'à réduire l'écart qui subsiste, en terme de qualité d'habitat, entre les parterres de coupe et les brûlis récents.

2.5 Travaux futurs

Notre étude a permis de mettre en lumière, entre autres, les effets qu'engendraient les lisières de coupes sur le comportement du Pic à dos rayé en forêt boréale. Toutefois, mis à part l'étude de Fayt (1999), les connaissances acquises sur la distribution des proies de cette espèce sont à ce jour assez limitées. Ainsi, des travaux portant sur la distribution des proies

préférentielles du Pic à dos rayé en fonction de la distance aux lisières amélioreraient la compréhension du comportement observé dans la présente étude.

Finalement, peu d'information existe concernant le choix de l'emplacement de nidification pour cette espèce. En effet, aucune étude empirique n'a encore été conduite pour le Pic à dos rayé dans le but de déterminer si les individus de cette espèce évitent les habitats de lisière lors du choix d'un site de nidification. Il serait par conséquent intéressant, dans un futur projet, de mesurer la sélection des substrats de nidification par les pics à dos rayé en fonction de leur distance aux bordures de coupes, ainsi qu'à la taille des peuplements forestiers résiduels à l'intérieur desquels ils sont situés.

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